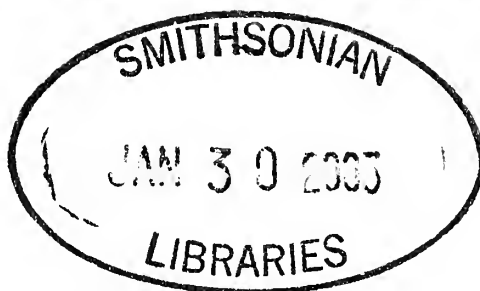
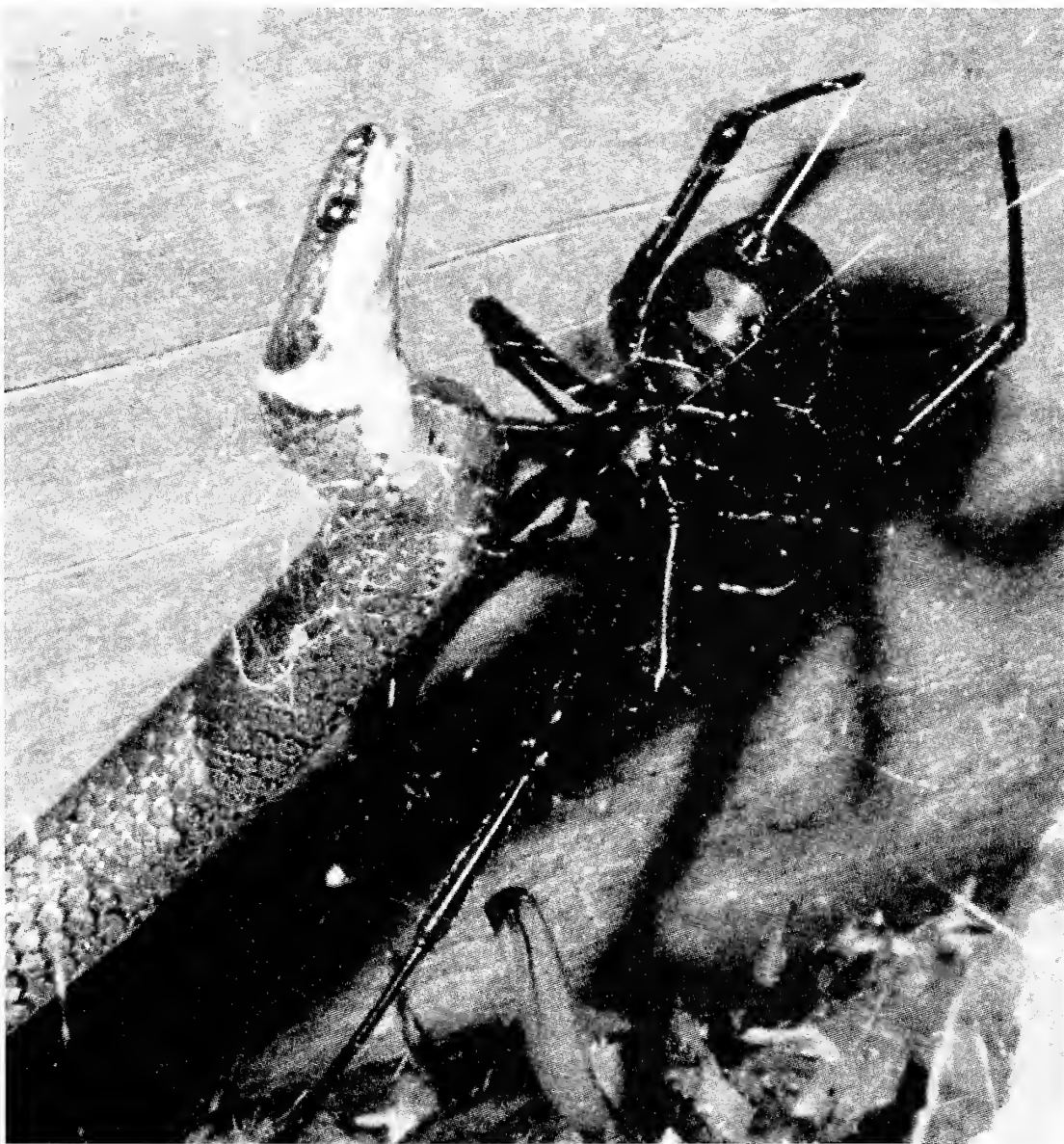


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Cover photo: Female *Latrodectus mactans* Frabricius 1775 catching a Ringneck Snake (*Diadophis punctatus*). Photo by Gail Stratton, University of Mississippi

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STYLOCELLUS RAMBLAE, A NEW STYLOCELLID (OPILIONES, CYPHOPHTHALMI) FROM SINGAPORE, WITH A DISCUSSION OF THE FAMILY STYLOCELLIDAE

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ABSTRACT. A new *Stylocellus* from Singapore, the smallest species of the genus, is described and fully illustrated. The family Stylocellidae is rediagnosed and emended to include the representatives of the genera *Miopsalis* and *Fangensis* based on the results of a phylogenetic analysis of the cyphophthalmid genera (Giribet & Boyer 2002).

Keywords: Cyphophthalmi, Stylocellidae, *Stylocellus*, *Miopsalis*, *Fangensis*, *Leptosalis*

Hansen & Sørensen (1904) proposed the subfamily Stylocellini [sic] to include the genera *Stylocellus* Westwood 1874, *Ogovia* Hansen & Sørensen 1904, and *Miopsalis* Thorell 1890. The subfamily was raised to the full family status and emended to include only the genus *Stylocellus* (Shear 1979), and was later diagnosed (Shear 1980). The genus *Stylocellus* comprises about 24 described species of mostly large Cyphophthalmi inhabiting the tropical areas of southeast Asia including the Malay Peninsula and Malay Archipelago (Sumatra, Borneo, Java, Sulawesi and Palawan), and the Philippines (Giribet 2000; Hansen & Sørensen 1904; Rosas Costa 1950; Shear 1993). An unidentified species has also been reported from northern Thailand (Suzuki 1985) and recent material has been collected in the Malay Peninsula in Thailand by P. Schwendinger (pers. comm.).

The genus *Stylocellus* was established by Westwood, who described *S. sumatranus* from the island that gave the specific epithet (Westwood 1874). Other species followed from Borneo (Pocock 1897) and Java (Thorell 1882). Hansen and Sørensen (1904) revised the genus and added descriptions of five new species. Two additional species were later described from the Malay Peninsula and Borneo (Roewer 1942). W. A. Shear recently described twelve species of *Stylocellus*, doubling the number of described species (Shear 1979, 1993), and M. Rambla described another species from a cave system in Borneo (Rambla 1991).

Leptosalis beccarii Thorell 1882 was described based on material from Mount Singalang in Sumatra (Indonesia). Subsequently, the species was erroneously synonymized with *Stylocellus sumatranus* Westwood 1874 (Thorell 1890/91). Despite its explicit treatment as a valid species by Hansen and Sørensen (1904), I mistakenly considered it a synonym of *S. sumatranus* (Giribet 2000). Clearly, *Leptosalis beccarii* and *Stylocellus sumatranus* are two separate species that differ at least in their cheliceral morphology, *L. beccarii* bearing an unusual second ventral process on the basal article. All stylocellids, and most cyphophthalmids, have a ventral process on the chelicera while *L. beccarii* and the new species here described share the apomorphic condition of having a second ventral process (see Fig. 6). This extra ventral process has also been found in many other members of the genus *Stylocellus*, in *Fangensis leclerci* Rambla 1994, and in one putative new species of *Miopsalis* Thorell 1890.

Currently, stylocellids comprise the single genus *Stylocellus*, which contains all the Cyphophthalmi with eyes, and excludes all eyeless species of the suborder. The genus (and family) was diagnosed by Shear (1980) as follows: “Eyes present. Ozophores type 2. First coxae free, second coxae fused to third. Abdominal sternites eight and nine and tergite nine all free. Chelicerae distally attenuate, with dorsal crest, cheliceral teeth uniformly large. Ovipositor (when studied) with sense

organs. Male lacking anal glands and modifications of the anal region. Adenostyle short, triangular, thornlike; male tarsus 4 entire. Penis of *Stylocellus* type."

Miopsalis pulicaria Thorell 1890 is a species of Cyphophthalmi found in Southeast Asia that has been considered a *nomen dubium* by previous authors due to the deficient description, based probably on a female. I have not been able to examine the type material of the species, of about 2.2 mm in length, supposedly lodged in MCSN. A specimen of a small cyphophthalmid from Mulu National Park (Sarawak, Borneo) resembling a *Stylocellus* but lacking eyes has been recently reported as a possible representative of the genus *Miopsalis* (Shear 1993). I have examined this single female specimen, deposited in BMNH, and it presents all the characters of typical *Stylocellus* except for the eyes. This specimen is considerably smaller than *M. pulicaria*, measuring about 1.6 mm. Unfortunately, no males of this unnamed species are known. I have also examined a male specimen (1.4 mm) of a possible second undescribed species of *Miopsalis* from the Kapit District, also in Sarawak (deposited in FMAC), and again it presents all the typical stylocellid characters except for the eyes.

Fangensis leclerci is an interesting cyphophthalmid described from northern Thailand (Rambla 1994), occurring near the geographic area of the juvenile *Stylocellus* reported by Suzuki (1985). Originally proposed to belong to the Sironidae, *Fangensis* displays many stylocellid characters, such as the fused second coxae and the typical stylocellid spiracles shaped as a letter "C". I have not been able to locate the specimens described by M. Rambla, but the original description of the animals seems to fit within the limits of *Stylocellus* except again for the lack of eyes, the cheliceral morphology, and in the presence of anal glands (Juberthie 1962, 1967), a character so far only found in Sironidae and Pettalidae (Shear 1980).

I have also examined material of an undescribed species collected by P. Schwendinger in Ko Siray, a small island off Ko Phuket (Thailand) that fits within the description of *Fangensis*, although this undescribed species is larger than *F. leclerci*. The juveniles of this species also lack eyes, but bear a red pigmented area behind the ozophores that resem-

bles a light sensitive organ, although this structure is not observed in the preserved juvenile specimens. I have not observed live adults, and therefore the existence of the "red spot" in the adults is unknown.

The examined specimens of *Miopsalis* and *Fangensis*, as well as the description of *Fangensis leclerci* made me evaluate the phylogenetic position of those taxa (see also the cladistic analysis of Giribet & Boyer 2002). In this article I describe the smallest *Stylocellus* known so far, from the Botanical Gardens of Singapore, and a new diagnosis of the Stylocellidae is proposed based on somatic characters, which should suffice to diagnose any adult specimen at the generic level.

METHODS

Abbreviations.—Specimens are lodged in the following institutions:

AMNH = American Museum of Natural History, New York (USA); BMNH = The Natural History Museum, London (UK); FMHD = Field Museum of Natural History, Chicago (USA); FMAC = Field Museum of Natural History, Arachnid collection, Chicago (USA); MCSN = Museo Civico di Storia Naturale 'Giacomo Doria', Genova (Italy); MCZ = Museum of Comparative Zoology, Harvard University, Cambridge (USA); MHNG = Muséum d'histoire naturelle, Genève (Switzerland); SMF = Senckenberg Museum, Frankfurt am Main (Germany); WAM = Western Australian Museum, Perth (Australia); ZMB = Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Berlin (Germany); ZMUC = Zoological Museum, University of Copenhagen (Denmark).

Diagnosis of Stylocellidae.—Eyes present or absent. Ozophores type 2. First coxae free, second coxae fused to third. Fourth coxae of the male meeting in the midline. Spiracles in the form of a capital "C". Lack of male sternal secretory glands. Abdominal sternites eight and nine and tergite nine all free. Chelicerae with dorsal crest and one or two ventral protuberances, but variable in relative length and shape. Distal segment of the chelicerae ornamented near the base to almost entirely. Cheliceral teeth uniform. Modifications of the anal region absent. Male anal glands may be present (as in *Fangensis*) or absent (as in *Stylocellus* and *Miopsalis*). Male tarsus IV entire with short adenostyle tipped with a tuft

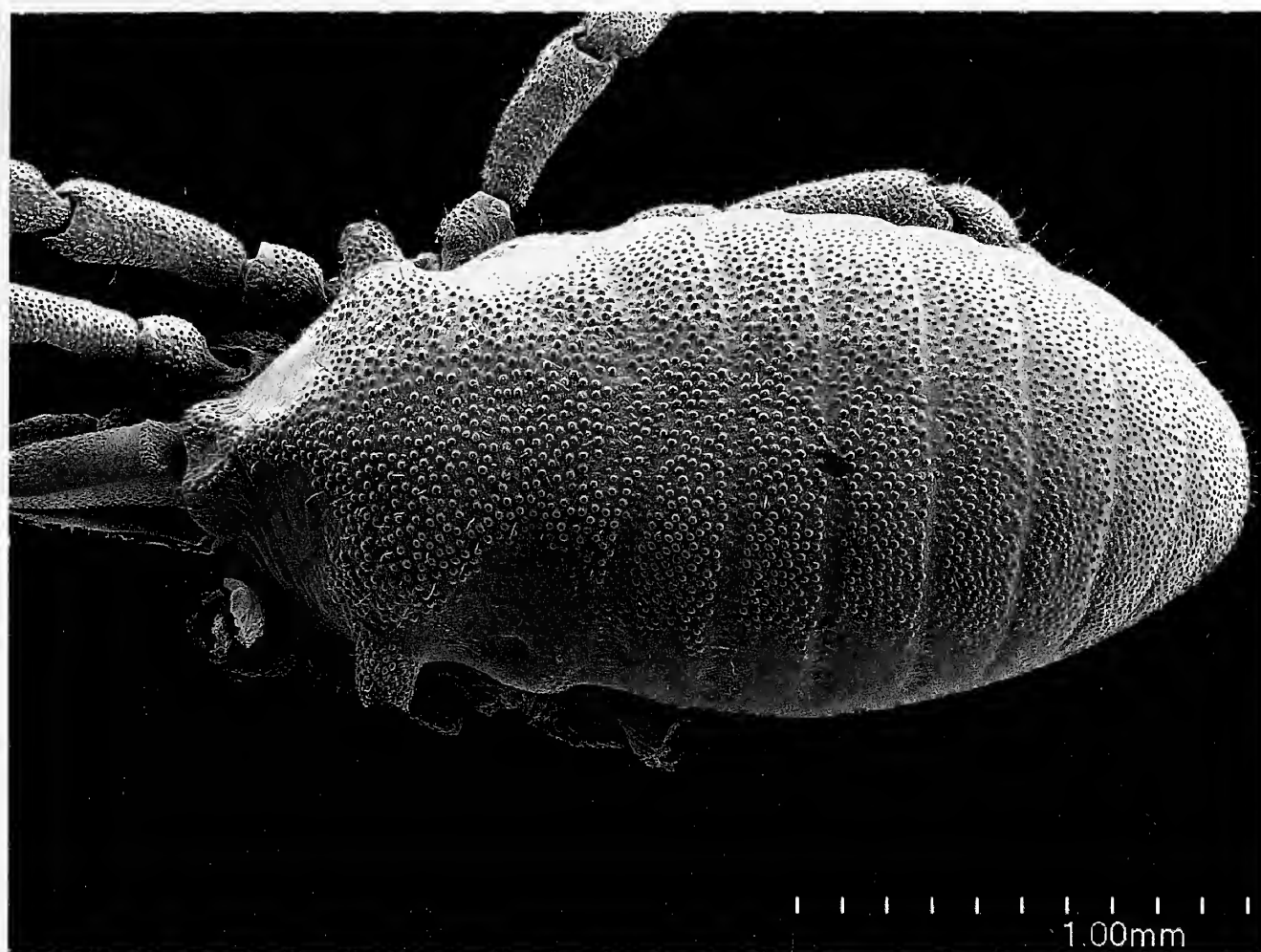


Figure 1.—Female *Stylocellus ramblae* new species, dorsal view. Scale bar = 1 mm.

of setae dorsally, not emerging from near the tarsal joint. Tarsus of leg I with a subapical modification where sensory hairs concentrate. Tarsus of leg II almost entirely ornamented. Claws of walking legs smooth. Ovipositor (when studied) with sense organs.

Type genus.—*Stylocellus* Westwood 1874

Genera included.—*Stylocellus* Westwood 1874; *Leptopsalis* Thorell 1882/83 (as *Stylocellus*); *Miopsalis* Thorell 1890; *Fangensis* Rambla 1991.

Material examined.—*Stylocellus collinsi* Shear 1993 (BMNH[E] 1999.167), *S. dumoga* Shear 1993 (BMNH[E] 1999.168), *S. gryllo-pecus* Shear 1993 (BMNH[E] 1999.169), *S. hillyardi* Shear 1993 (BMNH[E] 1999.170), *S. javanus* (Thorell, 1882) (AMNH; BMNH 56.102), *S. kinabalu* Shear 1993 (AMNH), *S. leakeyi* Shear 1993 (BMNH[E] 1999.171), *S. lionotus* Pocock 1897 (BMNH 95.7.20.23), *S. modestus* Hansen and Sørensen 1904 (ZMUC), *S. mulu* Shear 1993 (BMNH[E] 1999.172), *S. pangrango* Shear 1993 (AMNH), *S. pocockii* Hansen & Sørensen 1904 (BMNH no Register No.), *S. sabah* Shear 1993 (BMNH[E] 1999.173), *S. silhavyi* Rambla 1991 (Rambla collection), *S. tambu-sisi* Shear 1993 (BMNH[E] 1999.174), *S. tho-*

rellii Hansen and Sørensen 1904 (ZMUC), *Stylocellus* sp. (Cokendolpher collection), *Stylocellus* sp. (ZMB 11495), *Fangensis* sp. (MHNG THMA-00/16), *Miopsalis* sp. (BMNH no Register No.), *Miopsalis* sp. (FMHD 72–310).

Stylocellus ramblae new species

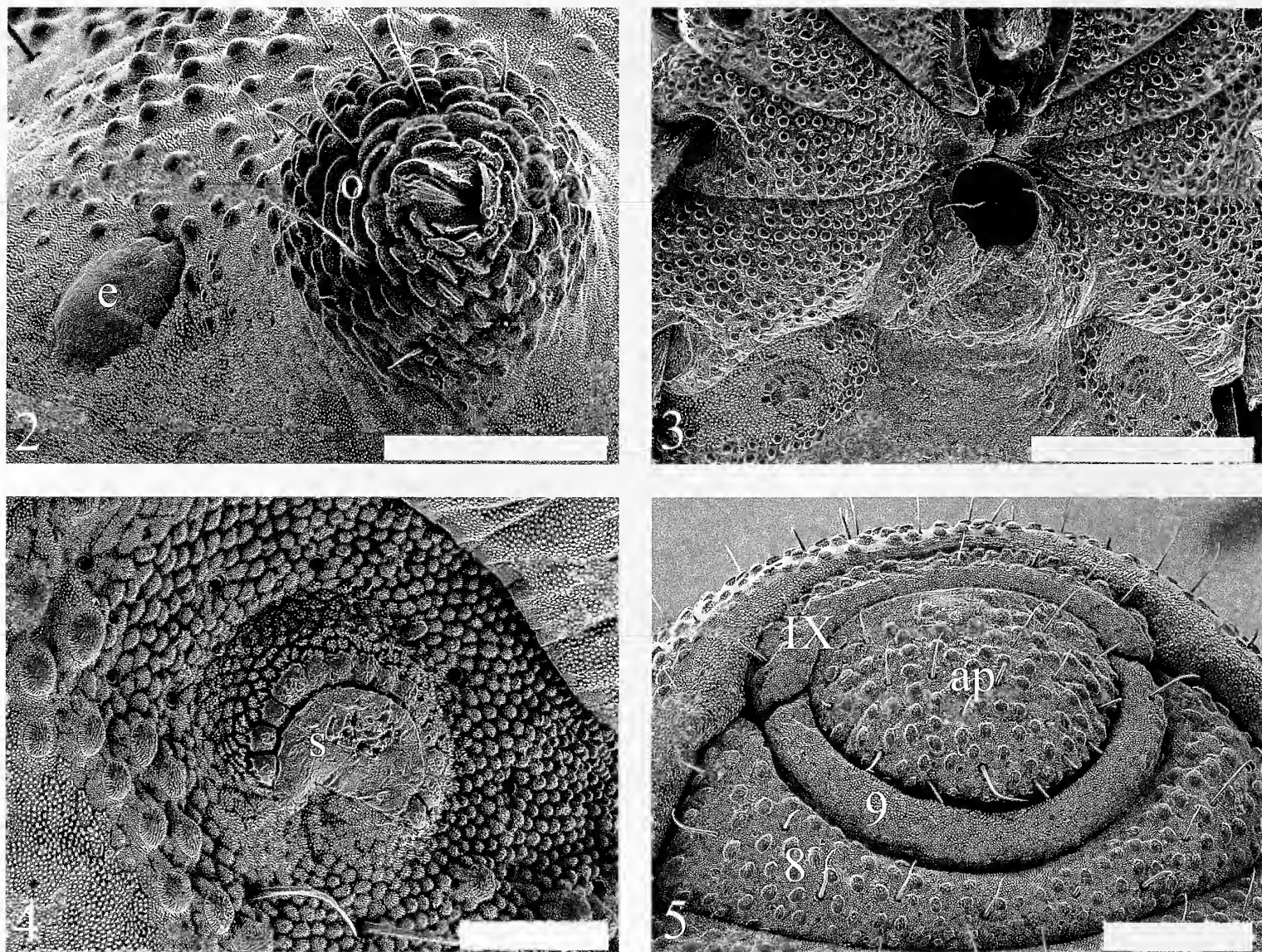
Figs. 1–20

Types.—Holotype male from the Singapore Botanical Gardens (Singapore), collected 8 April 1981 by J. Kethley, in forest litter and buttress litter (sample FMHD 81–274) deposited at the FMAC 1; two female paratypes (FMAC 2), same collection data; one female paratype mounted on a SEM stub (MCZ 35137); one female paratype from MacRitchie Reservoir (Singapore), collected February 1950 by G.H. Lowe, deposited at the WAM (Arachnological collection 94/181).

Additional material.—Six juveniles (FMHD 81–274), same collection data as holotype.

Etymology.—The species is named after my friend and colleague Maria Rambla, whose guidance inspired me to work on this fascinating group of Opiliones.

Diagnosis.—The species is related to other



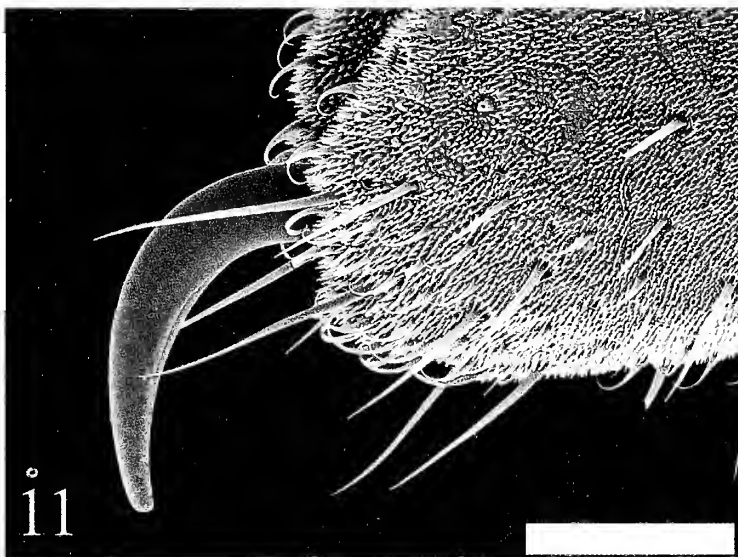
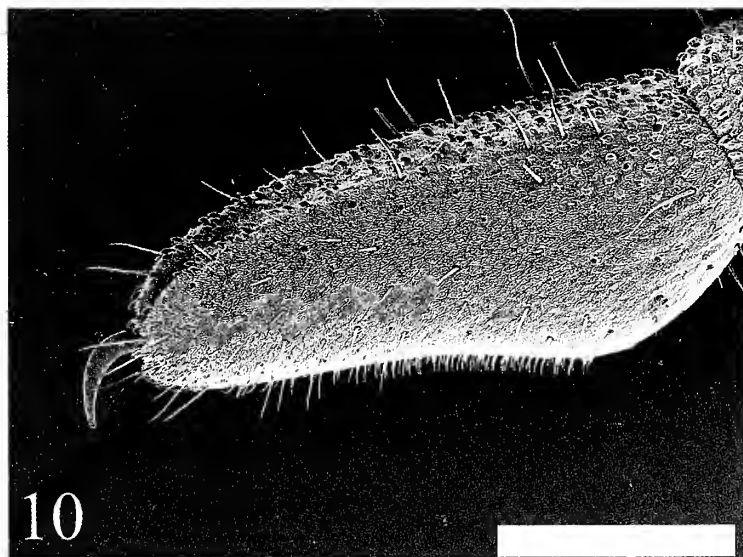
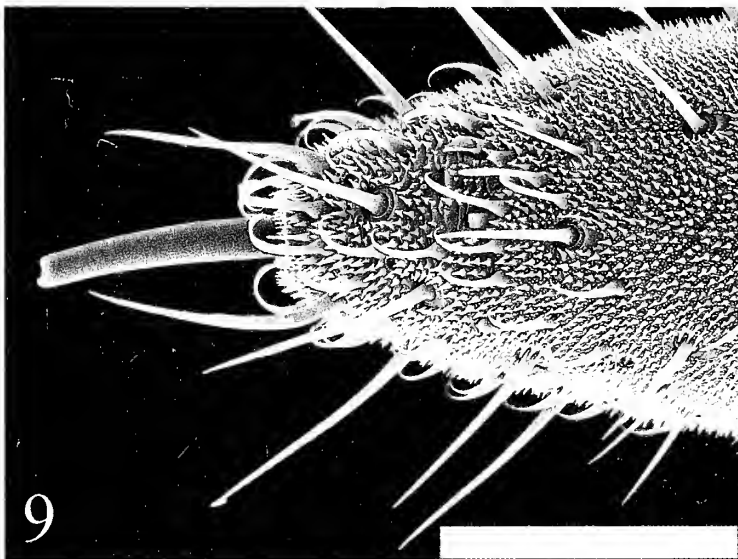
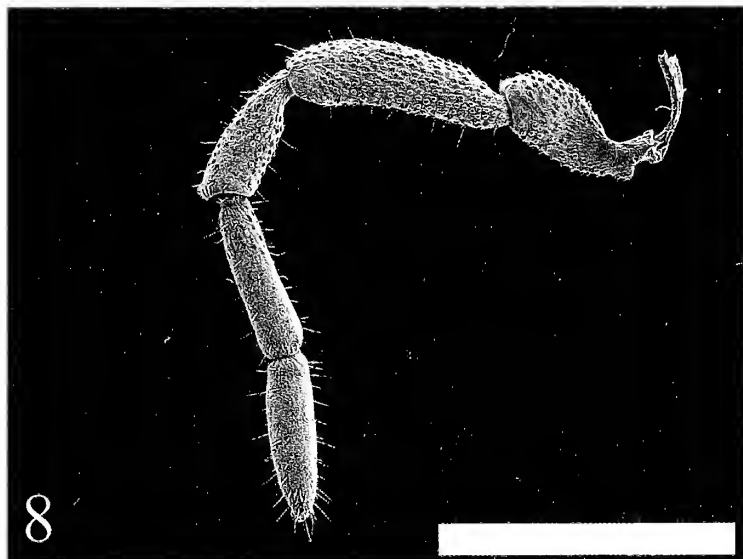
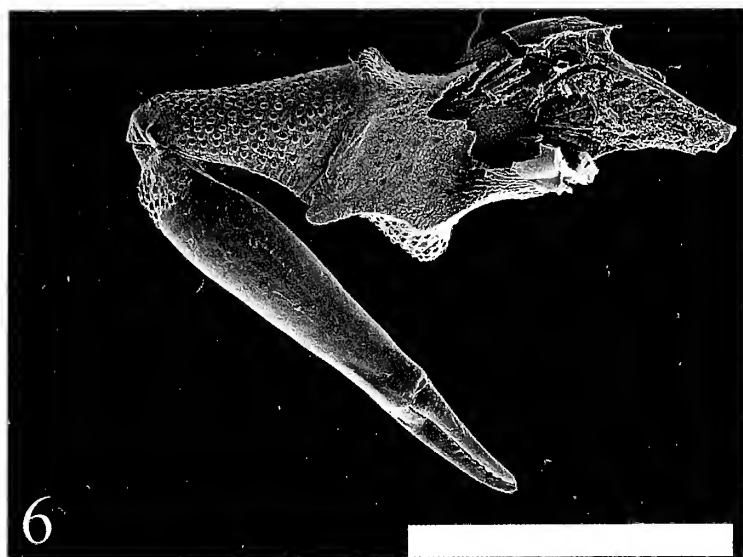
Figures 2–5.—*Stylocellus ramblae* new species, female: 2. Cephalic region in dorsolateral view showing the eye (e) and the ozophores (o); 3. Ventral thoracic complex; 4. Detail of the spiracular area with the spiracle (s) in the center; 5. Anal region showing the anal plate (ap) and the unfused sternites 8, 9, and tergite IX. Scale bars = 50 μm (Fig. 4), 100 μm (Figs. 2 & 5), 300 μm (Fig. 3).

stylocellids showing a similar cheliceral type, such as *Stylocellus beccarii* (Thorell 1882). The special morphology of the tarsus I (Fig. 10) clearly separates this species from any other stylocellids. The small size of the adult specimens, near 2.4 mm in length, is only comparable with that of *Stylocellus kinabalu* Shear 1993 from Borneo. However, *S. ramblae* is a smaller species, and the length/width ratio is higher than that in *S. kinabalu* (2.1 vs 1.73). The closest species geographically is *S. laevichelis* Roewer 1942, from Malakka (Malaysia), a much larger species whose description is not accurate and which I have not been able to examine.

Description.—Male holotype (FMAC 1) and female paratype (measurements refer to the female paratype studied with the SEM: MCZ 35137) Total length 2.41 mm, width across ozophores 1.10 mm, greatest width 1.14 mm, length/width ratio 2.11 (Fig. 1). An-

imal reddish when preserved in 80% EtOH with most of the dorsal body surface and legs almost completely granulated (Fig. 1). Anterior margin of cephalothorax without lateral projections, and with a subtriangular shape, the base of the triangle formed at the base of the ozophores, and with a truncated end. Small eyes (75 μm at maximum diameter) located anterior to the ozophores (Fig. 2). Ozophores subcylindrical with a folded structure in the opening and measuring 146 μm in diameter (Fig. 2). Ozophores completely nipped, with sensory hairs. Cephalothoracic transverse sulcus pronounced. Transverse abdominal sulci distinct, mid-dorsal abdominal sulcus not present (Fig. 1).

Coxa of leg I movable; coxa of the three remaining pairs of legs fused. Ventral thoracic complex of the male typical of stylocellids, with coxa III not meeting in the midline, and coxa II and IV meeting but not forming a long

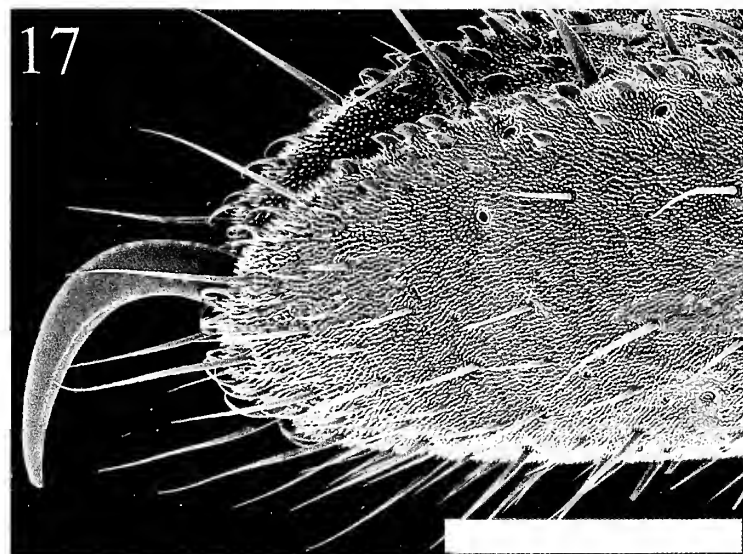
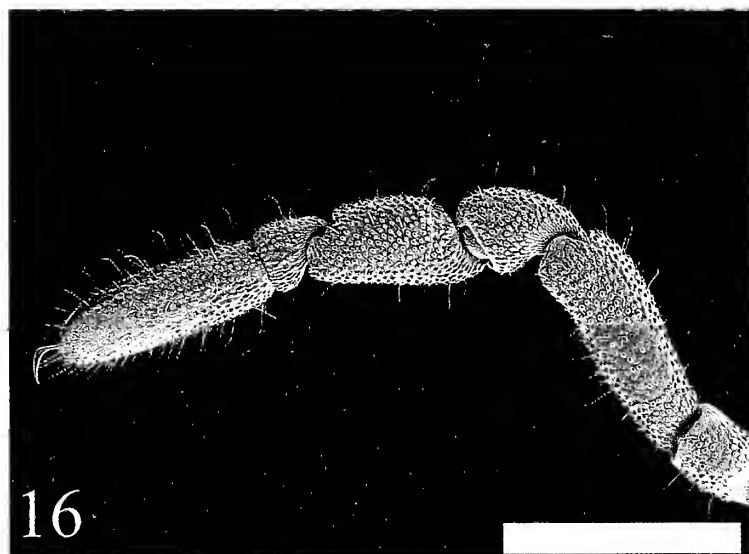
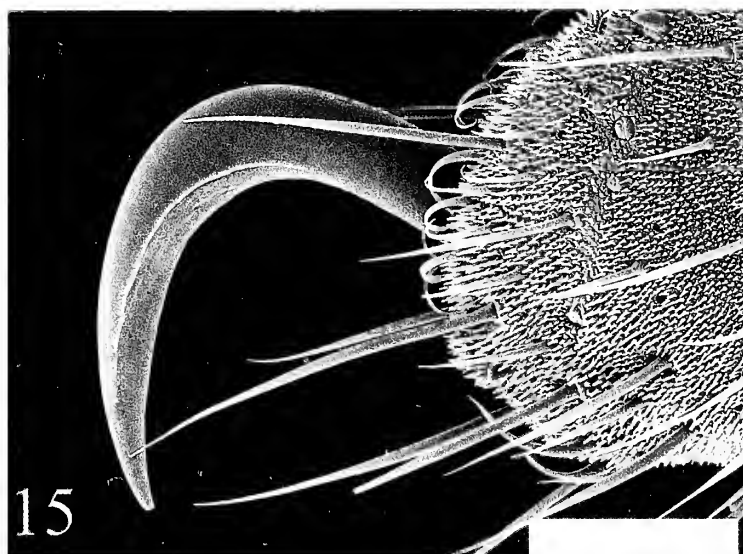
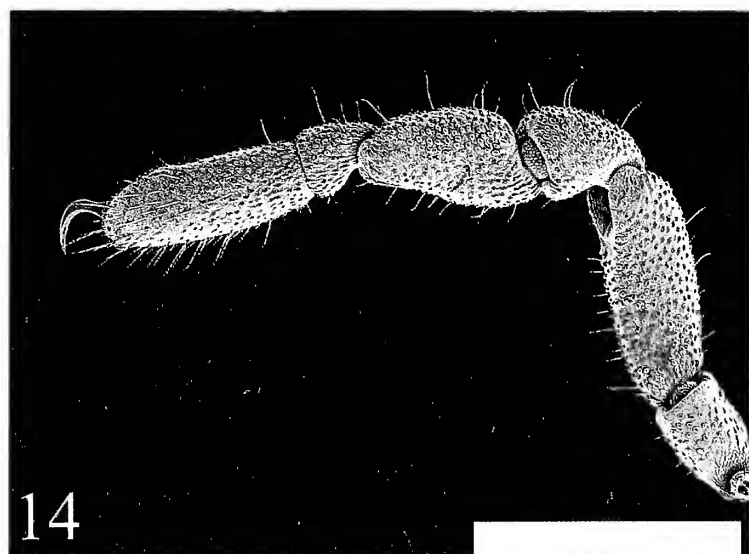
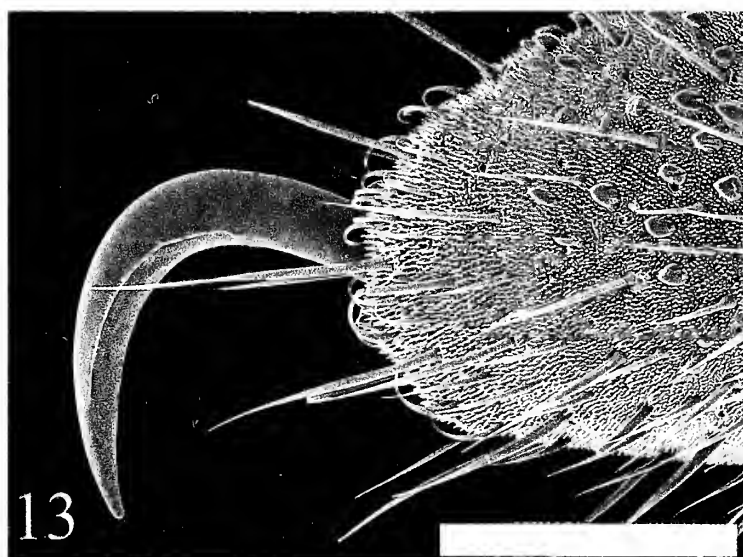
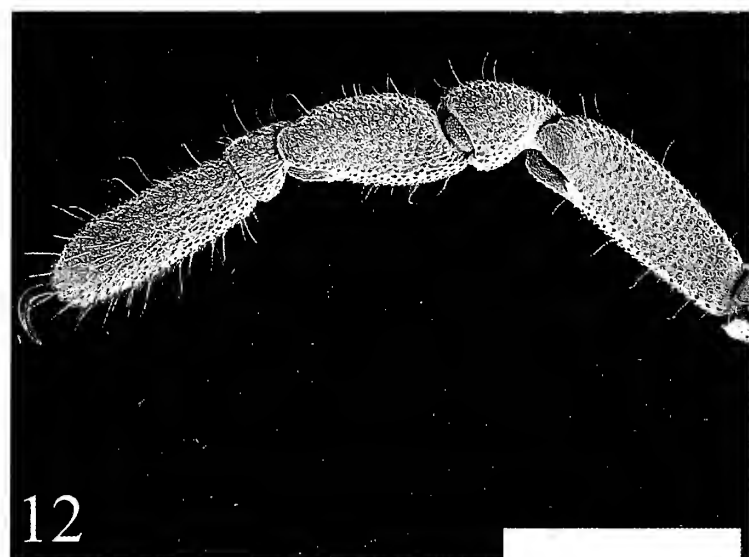


Figures 6–11.—*Stylocellus ramblae* new species, female: 6. External view of left chelicera showing the dorsal crest and the two ventral protuberances of the basal segment, and the ornamentation near the base of the distal segment; 7. Detail of the mobile digit and the dentition of the cheliceral distal segment; 8. Left palp; 9. Detail of the palpal claw; 10. Tarsal region of leg I; 11. Detail of tarsal claw I. Scale bars = 50 μ m (Figs. 9, 11), 100 μ m (Fig. 7), 200 μ m (Fig. 10), 500 μ m (Figs. 6 & 8).

midline area. Gonostome wider than long. Posterior wall formed by the first apparent abdominal sternite clearly distinct, like a genital operculum. Ventral thoracic complex of the female (Fig. 3) also typical of stylocellids, with only coxae III meeting in the midline,

while coxae IV adopt the typical tube-like shape directed anteroventrally.

Spiracles shaped like a capital letter “C” (Fig. 4) and enclosed in an area with special cuticular structures. Sternites 8 and 9 and tergite IX free, not forming a complete corona



Figures 12–17.—*Stylocellus ramblae* new species, female: 12. Leg II; 13. Detail of tarsal claw II; 14. Leg III; 15. Detail of tarsal claw III; 16. Female leg IV; 17. Detail of tarsal claw IV. Scale bars = 50 μm (Figs. 15), 100 μm (Figs. 13 & 17), 500 μm (Figs. 12, 14, 16).

analysis (Fig. 5). Male anal pore glands not detected and anal region not modified. Cuticle is granulated in all ventral areas, including coxae (Fig. 3) and anal region (Fig. 5).

Chelicerae short with the basal article granulated and presenting a dorsal crest and two ventral protuberances, the anterior one forming a ridge that unites it with the dorsal crest externally (Fig. 6). Distal article only orna-

mented near the joint, smooth otherwise. Total length of basal article 720 μm , length of distal article 800 μm , length of movable finger 240 μm . Dentition uniform and similar in both cheliceral fingers (Fig. 7).

Palps (Figs. 8, 9) with a ventral protuberance in the trochanter. Measurements of palpal segments (from basal to distal): 285, 395, 258, 298, 282 μm . Palpal claw 43 μm .

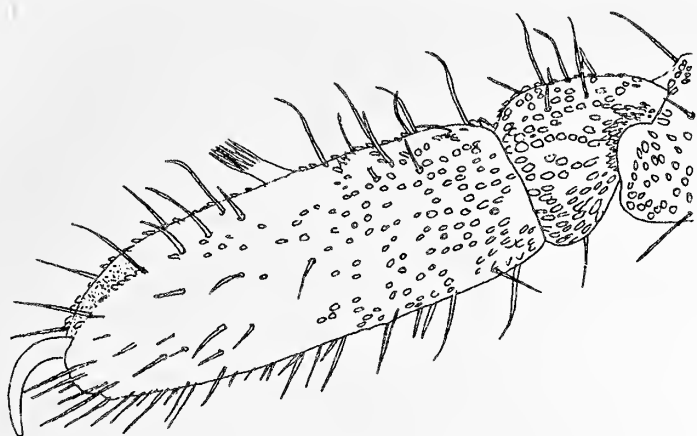


Figure 18.—Male tarsus IV showing the position of the adenostyle.

Legs with all claws smooth, without dentition or lateral pegs (Figs. 11, 13, 15 & 17). Surface of all articles, including metatarsi (= basitarsi) and tarsi (= telotarsi), clearly ornamented (Figs. 12, 14 & 16), except for the tarsi of leg I, where only the base and the dorsal surface are ornamented (Fig. 10). Tarsus of leg I swollen with a subapical modification with a concentration of sensory hairs that occupies about three quarters of the total tarsal length (Fig. 10). Tarsus IV of male entire with short adenostyle tipped with a tuft of setae dorsally at about halfway of the tarsal length (Fig. 18). Tarsus IV of female (Fig. 16) without modifications.

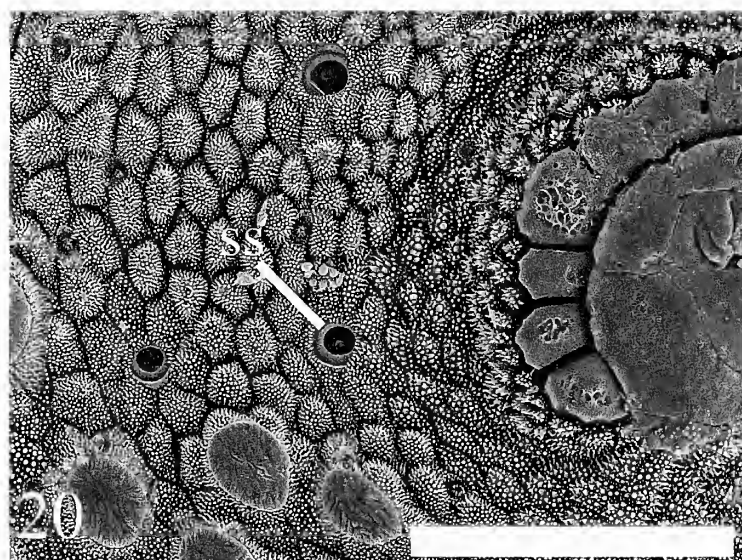
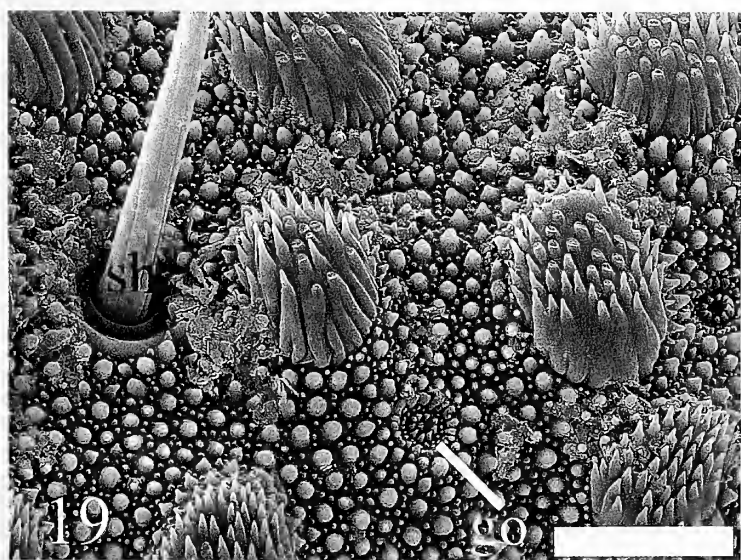
Penis (only the holotype is known) and ovipositor not studied.

Cuticular structures.—Cuticular structures of Cyphophthalmi have received attention recently through the use of SEM (Eisenbeis & Wichard 1985; Juberthie 1988, 1991;

Legg 1990; Pabs-Garnon 1977; Rambla 1991). In *Stylocellus ramblae* the ultrastructure of the integument reflects the presence of numerous special structures. The integument is primarily formed by three main structures covering the body (triple ornamentation of Rambla 1991), one matrix of small denticles surrounding larger denticles, and a series of nipples (more or less modified) distributed throughout the cuticle (Fig. 19). The large nipples are generally rounded smooth protuberances slightly striated at the flanks, but they undergo several modifications in different body regions. The nipples of the ventral region gradually become brush-like when moving towards the posterior end of the body, and especially in the anal plate (Fig. 19). This typical triple ornamentation is accompanied by two other common integumental structures, sensory hairs of about 5 μm at the base, and glandular openings of about 3 μm in diameter (Fig. 19).

The spiracular area has richly ornamented polygonal structures (Fig. 20). Large nipples, glandular openings, and sensory openings are accompanied by other putative sensory structures (Fig. 20) that look like the base of the sensory hairs found all over the body. The large nipples of the ozophores adopt an elongated shape towards the tip, but are round at the base (Fig. 2). The eye surface shows polygonal shapes, and it is completely covered of small denticles.

Distribution.—Known from the type locality, the Botanical Gardens of Singapore,



Figures 19–20.—*Stylocellus ramblae* new species, female: 19. Detail of the cuticular structures of the anal plate showing the typical triple ornamentation, the sensory hairs (sh) and the glandular openings (go); 20. Detail of the spiracular area showing different cuticular structures, including a putative special type of sensory structures (ss). Scale bars = 10 μm (Fig. 19), 50 μm (Fig. 20).

and from the MacRitchie Reservoir in Singapore.

Remarks.—This species is supposedly related to other Stylocellidae with a second ventral process in the basal article of the chelicerae, and probably with only the basal part of the distal segment of chelicerae ornamented. This also occurs in *Stylocellus beccarii* (Thorell 1882), *S. javanus* (Thorell 1882), *S. modestus* Hansen & Sørensen 1904, *S. dumoga* Shear 1993, *S. hillyardi* Shear 1993, *S. kinabalu* Shear 1993, *S. mulu* Shear 1993, *S. pangrango* Shear 1993, and *S. tambusisi* Shear 1993. Other species not properly illustrated in the literature or unexamined by me may also belong to this group.

DISCUSSION

Stylocellus ramblae clearly belongs to the family Stylocellidae, although its exact position within the family may require further investigation including all the putative stylocellid species. Preliminary data show that it is related to the clade having a second ventral process in the basal article of the chelicerae, a feature also shared with *Fangensis* and one species of *Miopsalis* (Giribet & Boyer 2002). I suspect that the type species of the genus, *S. sumatranus*, lacks the second cheliceral ventral process (as in *S. silhavyi* and *S. gryllospecus*), although I have not been able to examine specimens of this species. If this were confirmed, and all the stylocellids with the autapomorphic state were monophyletic, the resurrection of the genus *Leptopsalis* could be justified.

Penial characters have been widely used in cyphophthalmid taxonomy, including stylocellids (Hansen & Sørensen 1904; Rambla 1991, 1994; Shear 1979, 1993). Due to the uniqueness of the male holotype of *S. ramblae*, dissection for characterizing the penis seemed unwise since the species is easily diagnosed based on somatic and other secondary sexual characters.

Detailed SEM studies may reveal new characters to use in cyphophthalmid, and more specifically stylocellid, taxonomy and systematics. Pioneer work on stylocellid cuticular structures (Rambla 1991, 1994) together with the new data here presented suggest that an important number of characters are awaiting discovery and incorporation into the taxono-

my of this fascinating but yet character-poor group of Opiliones.

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HOW SPIDER ANATOMY AND THREAD CONFIGURATION SHAPE THE STICKINESS OF CRIBELLAR PREY CAPTURE THREADS

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ABSTRACT. Cribellar threads are primitive prey capture threads formed of thousands of fine, looped cribellar fibrils that surround larger, supporting fibers. Cribellar fibrils are produced from the spigots of an abdominal spinning field, the cribellum, which may be either a single, oval plate or a pair of medially divided plates. The number of spigots on a spider's cribellum is known to be directly related to the stickiness of its cribellar thread. Some spiders deposit cribellar threads in their webs as taut, self-supporting linear threads; others deposit looped threads along a supporting foundation thread. This study showed that the looped cribellar threads of *Kukulcania hibernalis* (Filistatidae) and *Mexitlia trivittata* (Dictynidae) were wider and stickier than linear threads produced by *Waitkera waitakerensis* and *Uloborus glomosus* (Uloboridae), respectively, that had the same numbers of cribellum spigots. Linear cribellar thread spun from the divided cribellum of *K. hibernalis* was both wider and stickier than linear thread spun from the undivided cribellum of *W. waitakerensis* that had the same number of spigots. A single cribellar plate of *K. hibernalis* and the cribellum of *Siratoba referena* (Uloboridae) had a similar number of spigots and produced cribellar threads with similar stickiness. Thus, both a spider's spinning anatomy and its spinning behavior affect the stickiness of its cribellar threads.

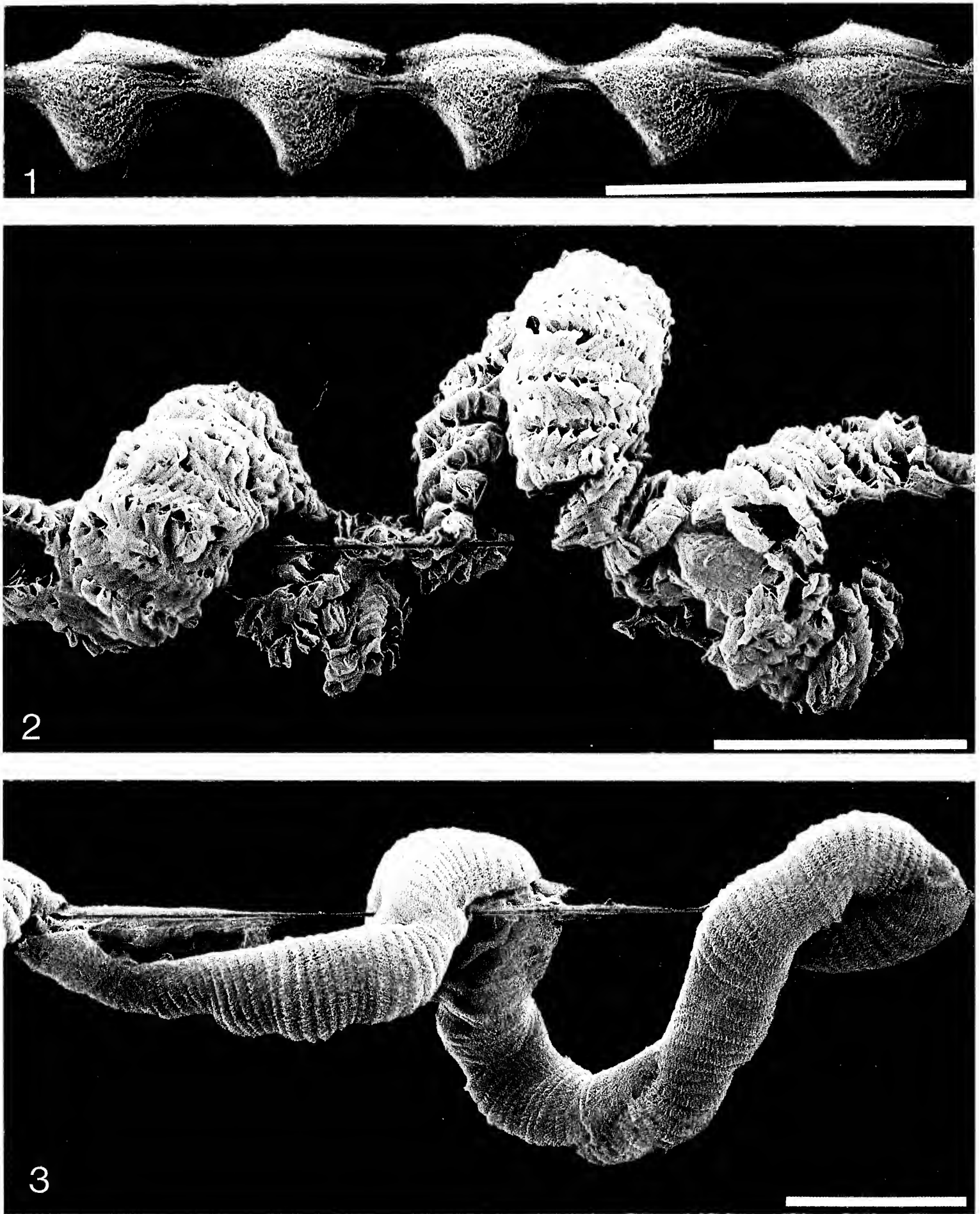
Keywords: Cribellum, spigot number, thread stickiness

Many spiders increase the effectiveness of their capture webs by incorporating sticky prey capture threads that slow or prevent the escape of insects from the web, thus giving a spider more time to subdue prey. These threads are of two types: dry, fuzzy cribellar capture threads (Eberhard & Pereira 1993; Opell 1994a, 1995, 1996, 1999a; Peters 1983, 1984, 1986) and viscous, adhesive threads (Opell 1997, 1998; Peters 1995; Tillinghast et al. 1993; Townley et al. 1991; Vollrath 1992; Vollrath et al. 1990; Vollrath & Tillinghast 1991). Cribellar threads are present in aerial webs constructed by the basal members of the large Infraorder Araneomorphae (Forster et al. 1987; Platnick 1977), whereas adhesive threads first appeared in the Araneoidea clade that includes modern orb-weaving spiders (Bond & Opell 1998; Coddington & Levi 1991).

The outer surfaces of cribellar threads (Figs. 1–3) are formed of thousands of fine, looped fibrils. These fibrils are spun from spigots on an oval spinning field termed the cribellum that is borne on the ventral surface of a spider's abdomen (Figs. 4–6; Kooor &

Peters 1988; Opell 1994b, 1999a; Peters 1992). Fibrils are drawn from the cribellar spigots by a setal comb termed the calamistrum that is located on the metatarsus of each fourth leg (Eberhard 1988; Opell 1994b, 1995, 1999a; 2001; Opell et al. 2000; Peters 1983, 1984, 1986). Rhythmic adductions of the posterior lateral spinnerets form the sheet of cribellar fibrils around supporting axial and auxiliary fibers to form a cribellar thread (Peters 1984) that often appears as a series of torus-shaped puffs (Fig. 1; Eberhard & Pereira 1993). Cribellar threads are still produced by representatives of all major araneomorph clades (Griswold et al. 1999) and are found in webs whose architectures range from sheet- and funnel-webs to cob-webs and orb-webs (Opell 1999). However, many araneomorph spiders have lost the cribellum and, with it, the ability to produce cribellar thread.

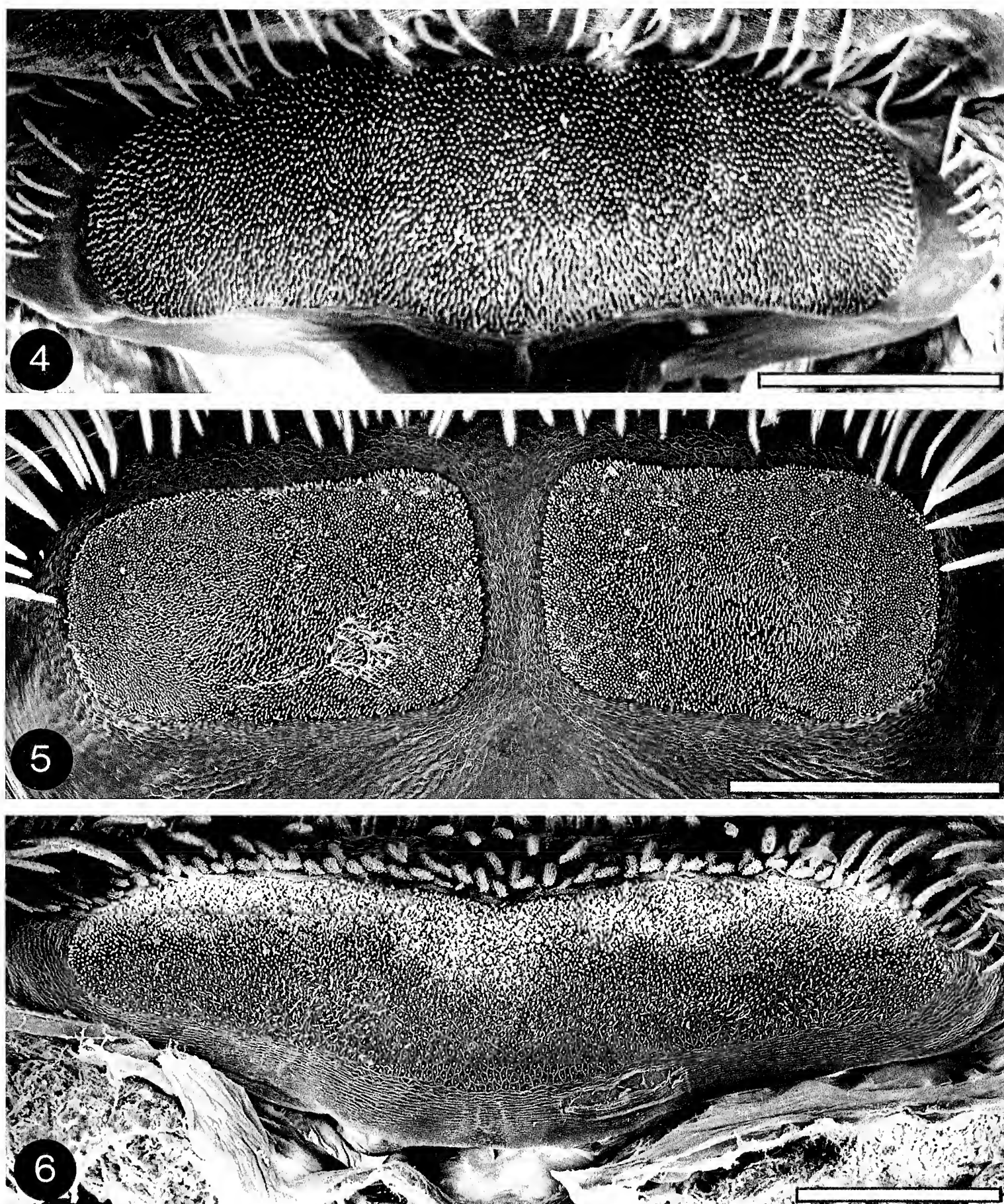
Cribellar threads are deposited in both their initial linear form and in a looped form (Fig. 1 and Figs. 2–3, respectively; Eberhard & Pereira 1993; Opell 1990, 1999a; Peters 1984, 1992). Linear threads are typically taut, self-supporting threads that run between non-



Figures 1–3.—Cribellar threads. 1. Linear thread of *Waitkera waitakerensis*; 2. Looped thread of *Kukulcania hibernalis*; 3. Looped thread of *Mexitilia trivittata*. Scale bars are 400 μm long.

sticky lines, such as the spirals of orb-webs produced by members of the spider family Uloboridae. However, in some webs they are deposited along a supporting non-sticky line, although usually for only short distances (Eberhard 1987; Opell 1982, 1990; Peters

1983, 1992). In contrast, looped threads are always laid down on non-sticky foundation lines that have been previously deposited (Eberhard 1988; Lubin et al. 1978). This makes it possible for a spider to fold and loop a strand of cribellar thread as it is being



Figures 4–6.—Cribella. 4. Cribellum of *Waitkera waitakerensis*; 5. Cribellum of *Kukulcania hibernalis*; 6. Cribellum of *Mexitlia trivittata*. Scale bars are 100 μm long.

pressed against the foundation line, and probably shifts much of the thread's support from its own axial and auxiliary fibers that lie within, to the foundation line on which the looped thread is placed.

There is an evolutionary premium on the stickiness of capture threads. An increase in the stickiness of linear cribellar thread was as-

sociated with the origin of orb-weaving spiders from non-orb-weavers (Opell 1999a) and with the reduction of the orb-web within the genera *Hyptiotes* Walckenaer 1837 and *Mia-grammopes* O. Pickard-Cambridge 1869 of the family Uloboridae (Opell 1994a, b). The evolutionary replacement of cribellar threads by adhesive capture threads in the Araneoidea

was also associated with an increase in thread stickiness (Opell 1997, 1998, 1999b). Inter-specific comparisons of linear cribellar threads show that cribellar thread width is also directly related to thread stickiness (Opell 1995).

These findings suggest that the spinning behavior that produces looped cribellar thread (Figs. 2–3) may be an alternative mechanism for increasing thread stickiness. By reconfiguring the native linear thread, this behavior increasing the thread's effective width, allowing it to present more cribellar fibrils per mm length to an insect surface. Thus, the stickiness of a looped cribellar thread should be greater than that predicted by the number of spigots on the spider's cribellum or by the width of its cribellum. To test this hypothesis, I compared the stickiness and widths of looped and linear cribellar threads produced by spiders with similar numbers of spigots on their cribella.

METHODS

Species studied.—*Kukulcania hibernalis* (Hentz 1842) (Family Filistatidae) occupies a silk-lined cavity from which a network of capture threads radiate, typically suspended a few mm to a cm above the substrate. *Mexitilia trivittata* (Banks 1901) (Family Dictynidae) constructs a silken retreat on low vegetation, logs, or other supports and spins a series of often long capture lines that radiate from the retreat. Both species produce looped cribellar threads (Figs. 2 & 3, respectively). *Waitkera waitakerensis* (Chamberlain 1946), *Uloborus glomosus* (Walckenaer 1837), and *Siratoba referena* (Muma & Gertsch 1964) belong to the Family Uloboridae and construct orb-webs. Webs of the first two species are typically horizontal, whereas those of the latter may be built at greater angles. These three species produce linear cribellar threads (Fig. 1).

Unlike the other species included in this study, *K. hibernalis* has a divided cribellum (Fig. 5). This, and the fact that its cribellar thread can be artificially reconfigured, make it a pivotal species for this study. The fibrils from each cribellar plate remain distinct as they are combed by the calamistrum and, in contrast to the looped cribellar thread of *M. trivittata*, that of *K. hibernalis* can be separated from the foundation line on which it rests and returned to a linear configuration.

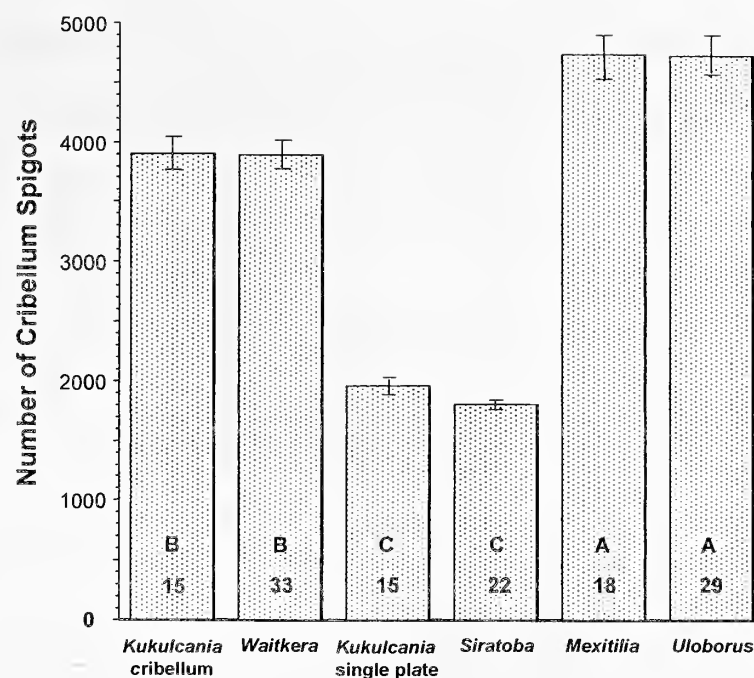


Figure 7.—Comparison of cribellar spigot number. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

The linear thread can then be separated into two strands, each formed of cribellar fibrils produced by one of the two cribellar plates. *Kukulcania hibernalis* and *W. waitakerensis* have similar numbers of cribellum spigots and the number of spigots on the cribellum of *S. referena* is similar to that on a single cribellar plate of *K. hibernalis* (Fig. 7). *Mexitilia trivittata* and *U. glomosus* have similar numbers of cribellar spigots (Fig. 7). Consequently, it is possible to make the three comparisons of cribellar thread stickiness shown in Table 1.

Only adult females were included in this study. The sample sizes for cribellum features, thread measurements, and thread stickiness values are given in Figures 7–11. For each species the same set of individuals was used for all the measurements, although for a few individuals not all measurements were available. Only one stickiness value per thread configuration per individual was included. I studied *K. hibernalis* at the Archbold Biological Station near Lake Placid, Florida; *M. trivittata* and *S. referena* at the American Museum of Natural History's Southwestern Research Station near Portal, Arizona; *U. glomosus* near Blacksburg, Virginia, and *W. waitakerensis* near Whangarei, New Zealand. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology.

Cribellum features.—I removed the cri-

Table 1.—Comparisons of the stickiness of cribellar threads and strands produced by cribella or cribellar plates with similar numbers of spigots.

Comparison	Species
Looped and linear cribellar threads	<i>Kukulcania hibernalis</i> vs. <i>Waitkera waitakerensis</i> <i>Mexitilia trivittata</i> vs. <i>Uloborus glomusus</i> <i>Kukulcania hibernalis</i> looped vs. linear.
Threads produced from entire and divided cribella	<i>Waitkera waitakerensis</i> vs. <i>Kukulcania hibernalis</i>
Threads produced from a single cribellar plate of a divided cribellum and an entire cribellum.	<i>Kukulcania hibernalis</i> vs. <i>Siratova referena</i>

bella of species whose thread features were measured, mounted them in water-soluble medium on microscope slides, and examined them under a compound microscope equipped with differential phase contrast (Nomarski) optics. For the divided cribella of *K. hibernalis*, I measured cribellum width as the distance between the lateral edges of the two cribellar plates. I included the space between the plates in this measurement because this is the functional width of the cribellum.

For the entire cribella of *M. trivittata*, *W. waitakerensis*, *S. referena*, and *U. glomusus*, I used a video camera and a computerized digitizing apparatus to measure the surface area of the cribellum and the density of approximately 50 spigots in each of three regions of the cribellum: anterior midline, lateral central region, and posterior lateral margin. I computed the number of cribellum spigots by multiplying surface area by mean spigot density. For the divided cribella of *K. hibernalis*, I measured the area of a single cribellar plate and determined the density of spigots in the median, central, and lateral regions of this plate. I doubled the number of spigots on a single plate to obtain the total number of cribellum spigots.

Cribellar thread features.—I collected cribellar threads from webs on microscope slides to which raised supports were glued. Double sided tape atop each support secured the thread at its native tension. The supports on thread samplers used for stickiness measurements were glued at 4.8 mm intervals. The thread widths of the three uloborid species were measured at 100 X under a compound microscope. *Kukulcania hibernalis* threads were measured at 25 X under a dis-

secting microscope and *M. trivittata* were measured at 40 X under a compound microscope.

I measured the stickiness of only recently spun threads that were not contaminated by dust or pollen, or damaged by a spider walking on them. These were collected from newly constructed orb-webs and from newly deposited capture lines of non-orb-weaving species. In the latter case, this was facilitated by partially destroying a web and looking each morning for new threads. I measured thread stickiness with a strain gauge that incorporates a glass or stainless steel needle (Opell 1993; 1994a). A contact plate made from a 2 mm wide piece of 320 grit, 3M® waterproof silicon carbide sandpaper was glued to the tip of this needle. The particles on the surface of these sandpaper plates are uniform in size and distribution (Opell 1993) and these plates registered the same stickiness for cribellar threads as did contact plates made from sarcophagid fly wings (Opell 1994a). Thus, a sandpaper contact plate registers stickiness values similar to that of a representative insect surface.

A motorized advancement mechanism pressed the cribellar thread against a sandpaper contact plate at a constant speed (13.5 mm/min for threads from uloborids and 10.7 mm/min for the other two species) until a force of 19.61 μ N/mm of thread contact was achieved. The thread was then immediately withdrawn by this mechanism at a constant speed (14.0 mm/min for threads of uloborids and 10.4 mm/min for threads of the other two species) until it pulled free from the plate. The force registered by the strain gauge immediately before this occurred was divided by the contact plate's width (measured to the nearest 20 μ m) to yield stickiness, expressed as μ N

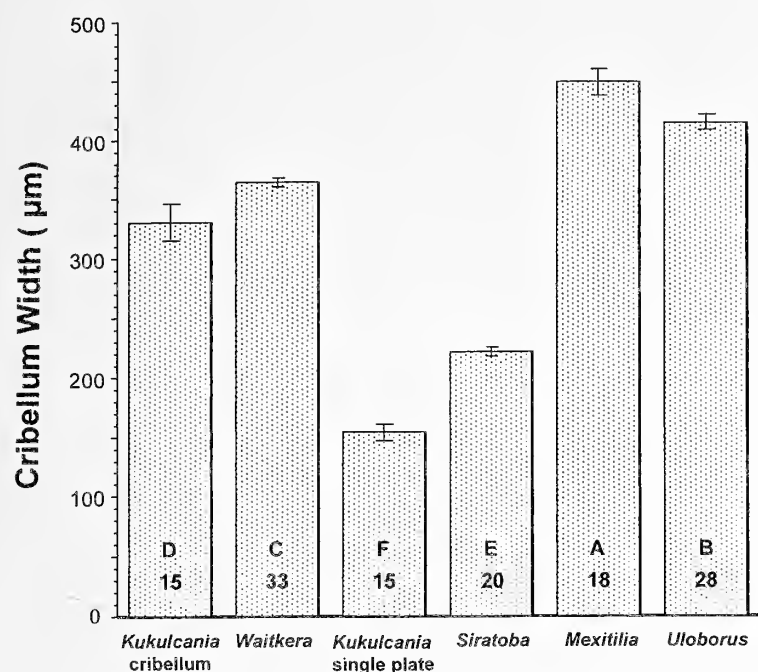


Figure 8.—Comparison of cribellum width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

of force per mm of thread contact with the sandpaper plate. The stickiness of four thread samples was measured for each specimen or, in the case of *K. hibernalis*, for each thread configuration, and their mean used as a spider's value.

Statistical analysis.—The normality of data was tested with a Shapiro-Wilk W-statistic (SW). I used a one way analysis of variance test (ANOVA) to determine if features differed among groups and a Ryan-Einot-Gabriel-Welsch multiple range test with $\alpha = 0.05$ (RGW, Day & Quinn 1989) to rank the values of features. These tests were performed with SAS for the Power Macintosh Computer (SAS Institute, Cary, North Carolina).

RESULTS

The number of spigots on each species' cribellum and on the single cribellar plate of *K. hibernalis* was normally distributed (SW $P > 0.26$). The means of these groups differed (ANOVA $F = 112.29$, $P = 0.0001$) and an RGW test (Fig. 7) supported the pairing of species described in Table 1. Cribellum width was also normally distributed for these groups (SW $P > 0.13$) and relationships among the groups' values (Fig. 8) reflect those of spigot number.

Thread width was not normally distributed for all groups. However, when log transformed it became so (SW $P > 0.07$) for all

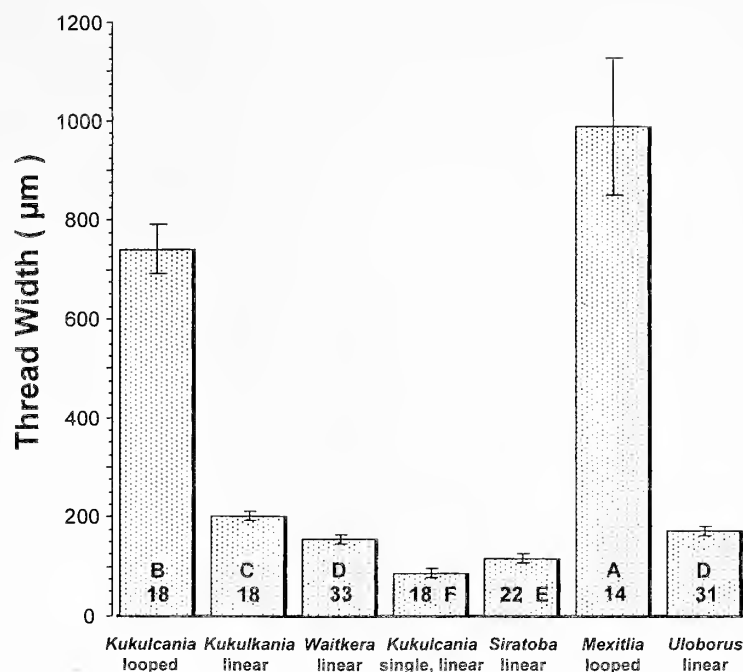


Figure 9.—Comparison of cribellar thread width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

groups but the single threads of *K. hibernalis*. These values could not be normalized, as 16 of the 18 values were identical. Transformed values differed among groups (ANOVA $F = 375.62$, $P = 0.0001$). An RGW test showed that the looped threads of *K. hibernalis* and *M. trivittata* were much wider than the linear threads produced by *W. waitakerensis* and *U. glomosus*, respectively, that had the same number of cribellum spigots (Fig. 9). The linear threads of *K. hibernalis*, *W. waitakerensis*, and *U. glomosus* had the greatest widths, and single-stranded threads of *K. hibernalis* and linear threads of *S. referena* had the smallest widths.

The ratio of cribellar thread width to cribellum width was not normal for all groups, but became so when log transformed (SWP $P > 0.18$). Transformed values differed among species (ANOVA $F = 41.79$, $P = 0.0001$). Their RGW rankings (Fig. 10) show that the looped threads of *K. hibernalis* and *M. trivittata* had a ratio of about 2.3, whereas single- and double-stranded threads of *K. hibernalis* and the linear threads of *W. waitakerensis*, *S. referena*, and *U. glomosus* had values that fell in the narrow range of 0.4–0.6.

Thread stickiness was not normally distributed for all groups but became so when log transformed (SW $P > 0.08$). Transformed values differed among species (ANOVA $F = 50.94$, $P = 0.0001$) and their RGW rankings

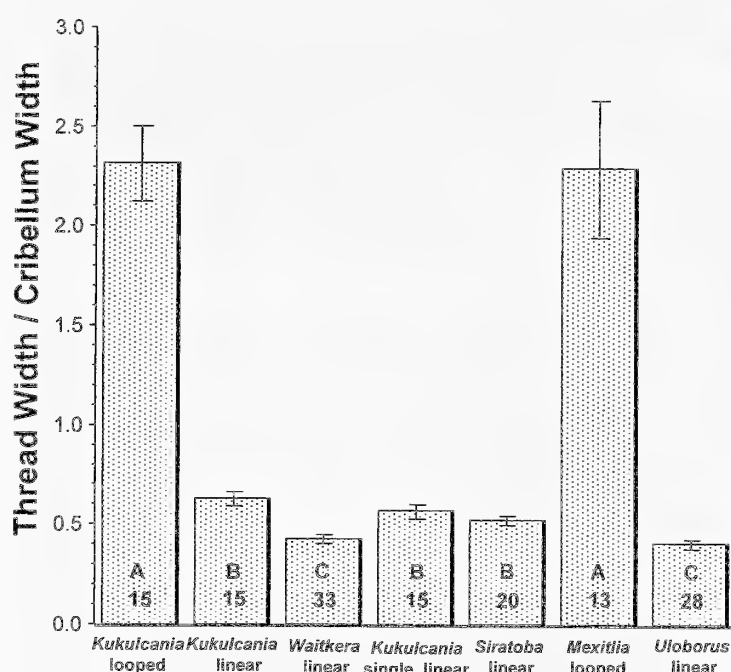


Figure 10.—Comparison of the ratio of cribellar thread width to cribellum width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

(Fig. 11, non-underlined letters) reflected those of thread widths. Looped cribellar threads of *K. hibernalis* and *M. trivittata* had the greatest stickiness, and the stickiness of double- and single-stranded *K. hibernalis* threads matched most closely those of *W. waitakerensis* and *S. referena*, respectively, with similar thread widths and similar numbers of cribellum spigots. When looped threads of *K. hibernalis* and *M. trivittata* were excluded, differences remained significant (ANOVA $F = 10.70$, $P = 0.0001$) and their RGW rankings (Fig. 11, underlined letters) showed that the stickiness of single-stranded *K. hibernalis* thread and *S. referena* thread had the same stickiness. However, the stickiness of double-stranded *K. hibernalis* thread exceeded that of the naturally linear thread of *W. waitakerensis*.

DISCUSSION

The results of this study show that a spider greatly increases the stickiness of its cribellar thread by depositing it in a looped fashion. The stickiness of linear cribellar thread is determined mainly by the number of spigots on a spider's cribellum (Opell 1994b, 1999a), whereas the stickiness of looped thread is shaped by a spider's spinning behavior. The looped threads of *K. hibernalis* are 2.1 times stickier than the linear threads of this species and 3.0 times stickier than the linear threads

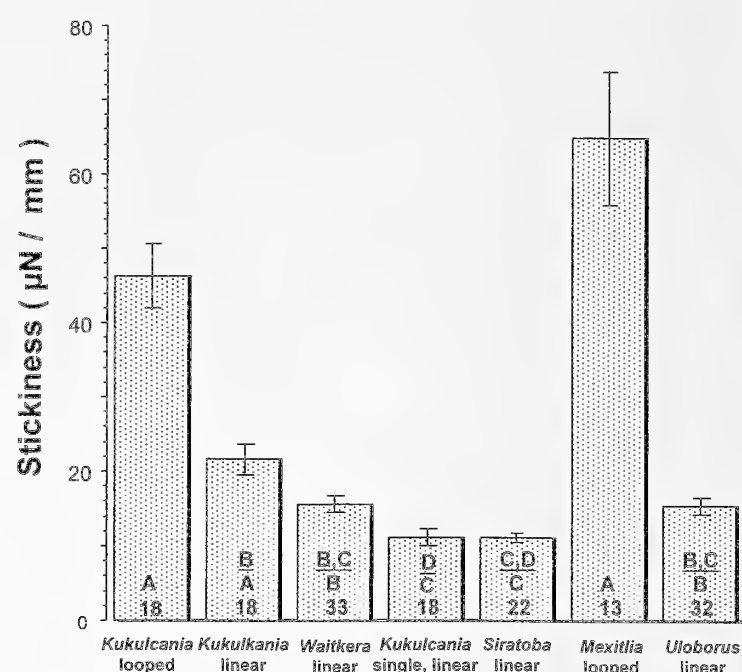


Figure 11.—Comparison of cribellar thread stickiness. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters within histogram bars denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test for all comparisons. Underlined letters rank the stickiness of the five linear cribellar strands and threads.

of *W. waitakerensis*, whose cribellum bears the same number of spigots. The looped threads of *M. trivittata* are 4.2 times stickier than the linear threads of *U. glomosus*, whose cribellum has the same number of spigots.

Among spiders that produce linear cribellar threads (or in the case of *K. hibernalis*, threads that can be made linear) thread stickiness mirrors thread width (Figs. 8 & 9). A formal analysis of this relationship is not possible due to the limited taxonomic representation and small sample size of this study and the inclusion of two types of artificially produced linear threads of *K. hibernalis*. However, positive Pearson correlations for thread width and thread stickiness among the seven threads studied ($r = 0.99$, $P = 0.0001$) and among the five linear threads ($r = 0.93$, $P = 0.02$) lend support to the hypothesis that cribellar thread width is an important determinant of thread stickiness.

The cribellum is a synapomorphy of the large Infraorder Araneomorphae (Forster et al. 1987; Platnick 1977) and first appeared as a single oval plate. A divided cribellum is found in a number of araneomorph taxa, and cribellum division appears to be a rather plastic trait. For example, in the genus *Mallos* O. Pickard-Cambridge 1902, the sister genus of *Mexitilia* Lehtinen 1967 (Bond & Opell

1997a), the plesiomorphic state is an undivided cribellum. However, in this clade of 14 species a terminal subclade of six *Mallos* species has as one of its synapomorphies a divided cribellum. Within this *Mallos* subclade, the divided cribellum has been reversed to a single plate in two sister species (Bond & Opell 1997b).

The relationship between cribellum width and cribellar thread stickiness may help explain the advantage of the divided cribellum of spiders like *K. hibernalis* (Fig. 5). By increasing the lateral spread of a cribellum's spigots, the divided condition may produce wider bands of cribellar fibrils that, when formed around supporting threads, produce wider and, therefore, stickier cribellar threads. Tentative support for this hypothesis comes from a comparison of the thread width, thread width/cribellum width ratio, and thread stickiness values of linear (double-stranded) *K. hibernalis* threads and *W. waitakerensis* threads (Figs. 9–11). These two species have cribella with the same number of spigots (Fig. 7), yet the linear thread of *K. hibernalis* has a greater thread width, thread width/cribellum width ratio, and stickiness than does *W. waitakerensis*. As the linear threads of *K. hibernalis* were produced by manipulating the spider's native looped cribellar threads, this conclusion must be interpreted cautiously and should be confirmed by studies of species that possess divided cribella and produce linear cribellar threads.

A different conclusion about the effect of cribellum division upon thread stickiness was reached by Bond & Opell (1997b). In a phylogenetic study that included four *Mallos* species with undivided cribella and two species with divided cribella, they found that cribellum width, surface area, and spigot number of all six species was directly related to carapace width. As cribellar thread stickiness is known to be related to cribellar thread width (Opell 1995) and cribellar spigot number (Opell 1994b), these authors found no support for the hypothesis that species with divided cribella produce stickier cribellar threads than species with undivided cribella. Although this and the present study draw conflicting conclusions about the effect of cribellar division on cribellar thread stickiness, neither resolves the question definitively.

Increasing cribellar thread stickiness re-

quires an increased silk investment. This may be achieved by increasing the number of fibrils that form a linear thread or by increasing the amount of linear thread that is folded to form a looped thread. Adult female *K. hibernalis* have a mass that is 37.2 times that of *W. waitakerensis* and adult female *M. trivittata* a mass that is 2.2 that of *U. glomosus* (Opell 1999a). Consequently, it is clear that spider size does not limit the number of spigots that a cribellum can bear and thus does not require a spider to produce looped threads in order to achieve greater thread stickiness. A number of non-orb-weaving spiders also produce linear cribellar threads (Opell 1999a), so web architecture also fails to provide a simple explanation for these two approaches. The prey capture performances of looped and linear threads probably differ more substantially than indicated by the stickiness measured in this study. Looped threads may be better adapted to fold around the appendages of an insect and, thus, achieve a greater area of contact than taut linear threads (Lubin et al. 1978). As insects struggle, loops may stretch and pull free from their foundation lines, helping to absorb some of the force generated by a struggling insect and making it more likely that the insect will contact other looped threads (Eberhard 1976; Opell 1990).

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BODY CONDITION AND MATE CHOICE IN *TETRAGNATHA ELONGATA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. The mate preference characteristics of adult *Tetragnatha elongata* were assessed with respect to measures of female mass, linear size (length), and condition (mass scaled by length: body condition). Males preferred longer, heavier females and females with higher body condition indices. When mass is partially controlled, males still preferred females of higher body condition, but reversed their preference for length and chose smaller females. We present evidence that female body condition and mass are associated with the volume of her egg load and the proximity of oviposition, whereas female body length is not associated with either. Females displayed no clear preference among males for mass or linear size, but were reluctant to mate in female-choice trials. The small sample size obtained may have obscured the detection of female mate preferences if they exist. This may be the first evidence that mate choice is influenced by body condition rather than mass or linear size among spiders.

Keywords: Mate choice, size, body condition, oviposition, *Tetragnatha elongata*

Body size is a signal used by many animals to assess the quality of a mate. Measurements of mate quality, including overall energy intake, genetic quality, and other components of fitness, are associated with larger body size in both sexes (Andersson 1994). Larger males often achieve higher mating success by winning competitions for mates or through pre- or post-copulatory mate guarding (Parker 1970). Females may benefit by choosing larger males because these males have higher lifetime mating success, higher genetic quality or more vigorous copulatory courtship (Eberhard 1991, 1996). Males may benefit by choosing larger females when larger females have higher quality offspring or greater fecundity (Andersson 1994).

For spider species, reproductive success for both sexes also seems to be influenced by body size (as measured by linear dimensions) and mass. Male body size has been associated with higher reproductive success in several spider species via larger males winning competitions for mates (Riechert 1978; Christenson & Goist 1979; Vollrath 1980; Austad

1983; Rubenstein 1987; Watson 1990; Hack et al. 1997). If this pattern holds true, where mate competition exists females should prefer larger males as mates when given a choice. Similarly, males should prefer heavier females as mates when female fecundity is associated with body mass. Female body mass has been associated with higher fecundity in spiders (Wise 1979; Briceño 1987; Vollrath 1987; Morse 1988; Uetz 1992; Head 1995) and other arthropods (Honek 1993; Spence et al. 1996). Males may also prefer heavier females because their greater mass may indicate that they are closer to oviposition. Mating with females immediately prior to oviposition may give males a reproductive advantage in species with sperm mixing or last-male sperm precedence (Parker 1970; Waage 1979; Miller 1984; Siva-Jothy & Tsubaki 1989; Parker & Simmons 1991; Birkhead & Moller 1998). Last-male sperm precedence is predicted for the orb-weaving spider, *Tetragnatha elongata* Walckenaer 1805 based on female reproductive morphology (Austad 1984; West & Toft 1999). Regardless of sperm precedence, mating closer to oviposition might also reduce the likelihood that a male will lose his gametic investment due to female mortality before oviposition.

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Recently, it has been argued that body condition is a better estimate of an animal's physiological state (and by extension, its fitness) than either linear size or mass (Jakob et al. 1996 and references therein). Body condition indices are a function of the mass of the animal, adjusted for its linear size, and may be particularly useful in measuring female spiders, as they cyclically mature and oviposit their eggs. While the female's linear size remains constant, her mass and body condition vary considerably over the course of this cycle, as her unsclerotized abdomen expands or contracts with feeding and starvation, yolk deposition or oviposition. Jakob et al. (1996) evaluated three different body condition indices using two spider species. They found that a condition index based on the residual index performed the best, and had the most straightforward biological interpretation (see Kotiaho 1999; Marshall et al. 1999 for further discussion). However, we are not aware of data to support the hypothesis that body condition *per se* (c.f., mass) correlates with fecundity in female spiders or with the timing of oviposition. It is also not known if body condition directly influences mate choice (independent of mass and/or linear size).

Here we examine the influence of linear size, mass, and body condition on mate choice in *T. elongata*. We also examine oviposition in female *T. elongata* to see how linear size, mass, and body condition correlate with measures of fecundity and the timing of oviposition.

METHODS

Natural history and collection.—Little is known about the natural history and mating behavior of *T. elongata* (Levi 1981; Gillespie 1987; Smallwood 1993). Individuals build orb webs over or near water throughout the eastern and southern United States (Levi 1981). They typically rebuild their webs daily and, in some circumstances, relocate almost as often (Gillespie & Caraco 1987; Smallwood 1993). Individuals exhibit aggregative behavior at high prey densities and often share silk lines, although not prey, in these groups (Gillespie 1987). They are nocturnally active spiders. During daylight hours, females rest beside their webs while adult males often move between aggregations of females (Danielson-François, pers. obs.). Both adult males and fe-

males live for several months and mate repeatedly. Females lay multiple egg sacs beginning two weeks after the final molt and continuing until death (Danielson-François, pers. obs.). Several generations may overlap during the warmer months.

The 105 adult *T. elongata* for the initial mating study and the oviposition study were collected along the banks of the Crum Creek in eastern Pennsylvania, Delaware County (39°37' N; 75°7' W) from June to September 1993 and 1994. An additional 144 adults were collected from the banks of Westhampton Lake in Richmond, Virginia (32°30' N; 77°32' W) from June to September 1998. These spiders were used to continue mating studies. The study sites were repeatedly sampled for spiders and as new adults matured they were collected. However, given the high frequency of mating these adults were unlikely to be virgins and, after collection, several females laid egg sacs that later hatched. While it would be ideal to use virgins in the study, at least in *T. elongata*, males and females do mate multiple times and males reinduct sperm (Danielson-François, pers. obs.). Separate sets of animals were used in the mating and oviposition studies.

Individual spiders were marked with bands of Testor's model paint and housed in clear acrylic aquaria (ranging from 40 L × 20 W × 15 H to 100 × 50 × 62 cm). Spiders were fed *ad libitum* (*Drosophila* spp. and Tipulidae spp.) for the mate choice study and for the oviposition study were kept on a standardized diet (eight *D. virilis* daily). Voucher specimens for the study are deposited in the collection curated by the Department of Entomology, University of Arizona, Tucson, Arizona, USA.

Linear size, mass and condition.—We measured the right femur of the first leg to the nearest 0.1 mm (as a measure of linear size) and weighed each adult collected to the nearest 0.001 g. We assigned each female a body condition score (BCS hereafter) by generating a residual index. The residual index was constructed by regressing log-transformed mass against log-transformed femur length following the methods of Jakob et al. (1996). BCS for an individual spider is its residual (positive or negative) from the regression. Residuals were analyzed and variance in the index was homogeneous across different linear sizes as

determined by visual inspection. Females with higher BCS are heavier for their linear size.

Mate choice trials.—Male preferences were assessed by introducing a male into an aquarium with two females of significantly different linear size and mass and observing his behavior. Collected females were divided visually into large and small linear size classes. The spiders were kept on a 12:12 light-dark cycle at room temperature. We conducted mate choice trials between 13:00–16:00 (dark period of the cycle) and observed the spiders under a dim red light.

We recorded both body length and mass for both female spiders in each trial. The longer females had significantly longer femurs than small females ($n = 78$, $\bar{x} = 12.90 \pm 0.13$ mm, $\bar{x} = 11.20 \pm 0.16$ mm, respectively; paired t-test; $t = 12.0$, $df = 77$, $P < 0.0001$). Heavier females weighed significantly more than lighter females ($n = 78$, $\bar{x} = 0.066 \pm 0.002$ g, $\bar{x} = 0.045 \pm 0.001$ g, respectively; paired t-test; $t = 13.7$, $df = 77$, $P < 0.0001$).

Each test pair of females was introduced into the tank at least one day before the trial to allow females to adjust to the tank and to spin a web. Some tanks had a partial partition dividing the tank into two halves, and all tanks were large enough for each female to build her own (albeit small) web. Males were placed between the females' webs. We recorded the linear size of female chosen (roughly, large or small) and the duration of the mating. If a male mated with both females, the order in which he copulated also was recorded. As males usually attempted to mate within minutes of being placed in aquaria, the trial was terminated if the male remained stationary and did not copulate within 1 h. Usually, males that did not mate wandered for a few minutes and then remained stationary and did not roam or contact the web strands.

Many spiders were used in more than one trial, but each trial was unique. No male was used more than 3 times, no pair of females was used more than twice, and no pair was ever tried against the same male more than once. A total of 93 males and 156 females were used in the mating trials.

Likewise, presenting a female with two males of significantly different linear sizes assessed female preferences. Males were separated into large and small linear size classes upon collection. Large males were signifi-

cantly longer than small males in femur length ($n = 11$, $\bar{x} = 0.06 \pm 0.02$ mm, $\bar{x} = 0.02 \pm 0.01$ mm, respectively; paired t-test; $t = 5.27$, $df = 10$, $P = 0.0004$). Heavy males weighed significantly more than lighter males ($n = 11$, $\bar{x} = 0.06 \pm 0.02$ g, $\bar{x} = 0.02 \pm 0.01$ g, respectively; paired t-test; $t = 4.97$, $df = 10$, $P = 0.0006$). Each female was placed in an aquarium and allowed to adjust to her enclosure and spin a web at least a day before the males were introduced. Two males were simultaneously placed on opposite sides of her web. Female choice was determined by observing until the female copulated with one of the males, or for one hour at which point the trial was terminated.

Oviposition.—Female *T. elongata* lay egg sacs continuously from two weeks after the final molt until death and are receptive to re-mating at any time, even the day before laying eggs. We predict that males will prefer heavier females, or those of higher body condition. This prediction is based on the assumption that such females are more fecund or closer to oviposition. Therefore, we tested female mass for an association with the timing of oviposition, the number of egg sacs laid, and a volumetric measure of the number of eggs in each sac. A separate group of 26 females was collected for studies involving the volume of the egg mass, while other analyses included females used in the mate choice trials. These females were fed a standard diet (eight *D. virilis* daily) which allowed them to gain weight slowly during the study. While each female was being weighed, her aquarium was checked for egg sacs. We recorded the number of egg sacs and the date laid for each female until she died.

Individual eggs were agglutinated and thus could not be counted; however, because the eggs were tightly packed together, we used the volume of the egg cluster the day it was laid as a measure of maternal investment. The volume of the egg cluster was calculated from the length, width, and height of the agglutinated eggs after the egg sac was stripped of silk. We examined the association between the volume of the egg cluster and the mass of the female from five days to one day before oviposition.

Statistical analyses.—For the mate choice trials, a binomial probability test was used ($p = q = 0.5$) with equal probability of mating

or not mating (Sokal & Rohlf 1995). Pairs of females or males used in mate choice trials were tested for significant differences in linear size using Student's paired *t*-test. ANOVA and simple linear regression were used to test for associations between female mass, egg cluster volume and number of days until next oviposition. All summary statistics of continuous variables are reported as $\bar{x} \pm \text{SE}$.

RESULTS

Mating behavior.—Overt courtship in *T. elongata* appeared very subtle or non-existent, contrary to that seen in most orb-weaving spiders (LeSar & Unzicker 1978; Robinson & Robinson 1980; Robinson 1982). Males positioned themselves at the edge of a female's web and made slight leg movements on the strands of the web. They often tapped the silk for a few seconds, paused with their first pair of legs resting gently on the web strand, then repeated the behavior until the female responded. Females almost instantly oriented to the male's vibrations and vibrated the web in response.

The vibrations of the female were either fast arrhythmic pulses or slower rhythmic pulses and seemed to predict her response to the male. When a female exhibited vigorous arrhythmic pulses, males approaching any further onto the web were chased away. Similar arrhythmic web vibrations were observed from a female as large prey became entangled in her web, prior to her attack on the prey. Only when the female pulsed rhythmically could the male approach her without interference. In the field, males would sometimes steal prey from female webs when the female exhibited slow rhythmic vibrations. More often, once a male made this initial contact with an accepting female, they paired immediately. As the male approached, both sexes spread their chelicerae and fangs apart. Within seconds the pair then vigorously grappled to interlock cheliceral fangs and assumed a ventral-to-ventral position for mating. The male used his 3rd pair of legs to contact the female's abdomen and often moved her into position, sometimes even shaking her until he successfully inserted his pedipalp.

Mating duration varied ($n = 77$, $\bar{x} = 416 \pm 31$ seconds). Once chelicerae were engaged, mating consisted of several alternating insertions of each pedipalp and was terminated by

cheliceral disengagement. During each insertion, the male inflated the hematodochae of his pedipalp repeatedly.

Females appeared to terminate matings. These terminations often occurred when the male was in the process of switching from one pedipalp to another. The female pressed her chelicerae together, bringing her fangs closer to the body of the male. The male used his 3rd pair of legs to press his body away from the female as she moved her chelicerae. Once the chelicerae were disengaged, the male quickly retreated from the web, while the female would remain where she had been mated. Sometimes, after mating, the female chased the male a short distance with her chelicerae and fangs spread open before returning to her former position. Occasionally, males were cannibalized after mating.

Linear size and mass.—Overall, females ranged in mass from 0.02–0.11 g ($n = 156$, $\bar{x} = 0.056 \pm 0.001$ g), and were significantly heavier than males who ranged from 0.01 to 0.08 g ($n = 93$, $\bar{x} = 0.034 \pm 0.001$ g) in mass ($df = 247$, unpaired $t = 11.67$, $P \leq 0.0001$). Males ranged in femur length from 6.95–20.0 mm ($n = 93$, $\bar{x} = 12.47 \pm 0.18$ mm), while females exhibited a significantly smaller range from 7.0 to 15.1 mm ($n = 156$, $\bar{x} = 12.05 \pm 0.12$ mm) in femur length (unpaired $t = -1.99$, $df = 247$, $P = 0.048$). Both male femur length and mass ($r^2 = 0.27$, $F_{1,90} = 32.6$, $P \leq 0.0001$; Fig. 1) and female femur length and mass had a significant positive association ($r^2 = 0.45$, $F_{1,154} = 126.2$, $P \leq 0.0001$; Fig. 1).

Characteristics of mate preference.—We conducted 107 trials in which males were presented with a choice between two females. Mating occurred in 78 trials, usually within a few minutes. In unsuccessful trials, males did not seek females but instead remained stationary for one hour, after which the trial was ended.

Males showed a significant preference for females based on their mass, linear size, and BCS (Table 1). Mass, linear size, and BCS are related. In an attempt to tease apart the effects of each, we examined a subset of trials, those where the mass difference between the females was less than 20%. We chose the 20% cutoff in an effort to minimize the effects of mass, while still leaving a useful sample size. For the female pairs with less than 20% dif-

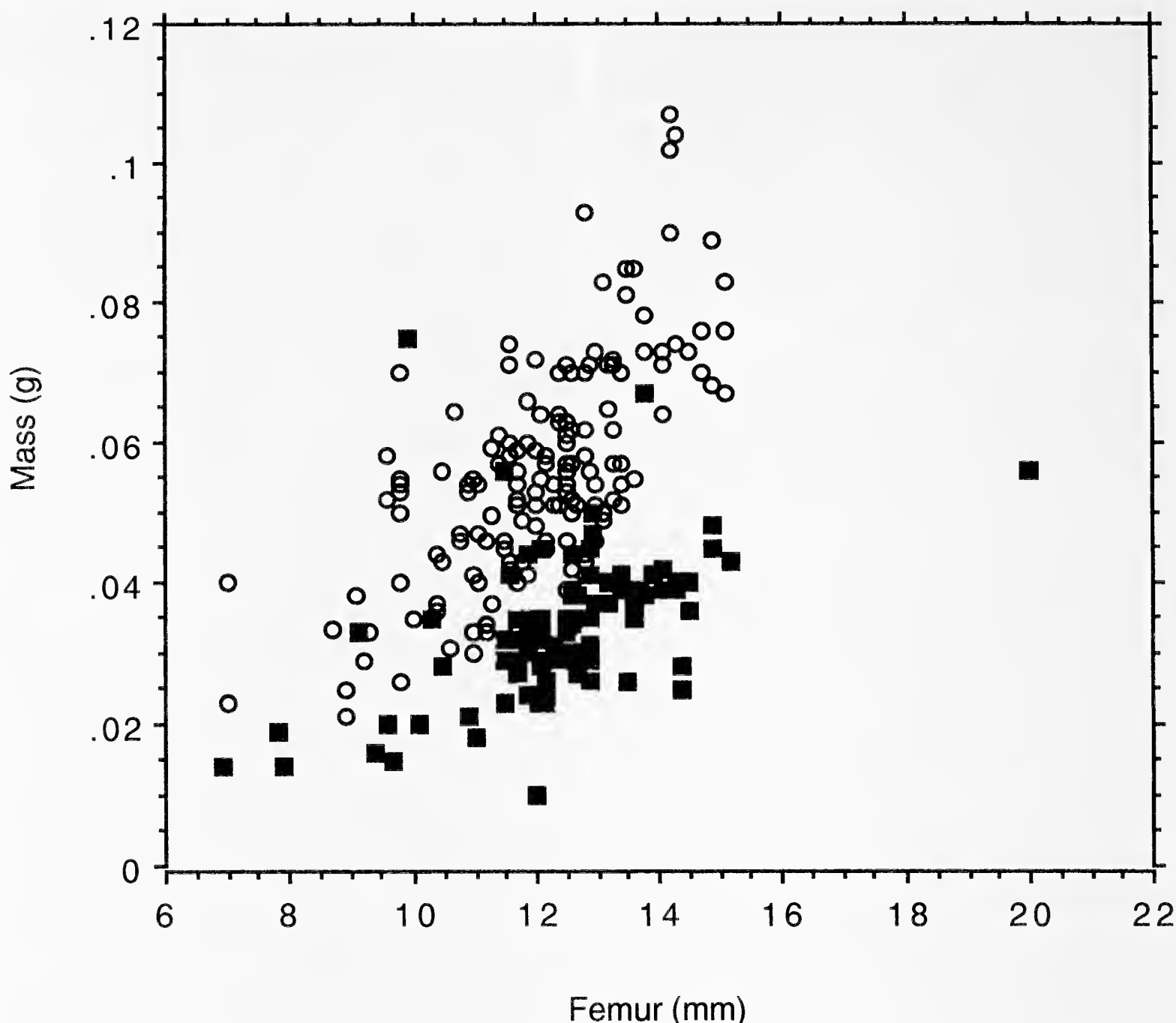


Figure 1.—Relationship between *T. elongata* mass and femur length of both females (open circles, $n = 156$) and males (filled squares, $n = 93$).

ference in mass, males exhibited no preference for heavier or lighter females. With mass partly controlled, males showed no preference for females based on their linear size. In fact, males preferred females of smaller linear size over longer females (Binomial test, $P = 0.0327$, Table 1). Smaller females of nearly the same mass are necessarily heavier in proportion to their linear size—in other words, they have a higher BCS. With the variation in mass minimized (less than 20% difference), males exhibited a significant preference for females of higher body condition (Binomial test, $P = 0.0328$, Table 1). We were not able to conduct a similar analysis minimizing variation in body condition, because there were only 3 cases where BCS differed by less than 20%.

Mated females had significantly higher body condition indices than unmated females ($n = 78$, $\bar{x} = 0.055 \pm 0.021$, $\bar{x} = -0.055 \pm 0.026$, respectively; ANOVA, $F_{1,154} = 10.85$, $P = 0.0012$). The variance of the residuals (the body condition scores) was homogeneous across different linear sizes as determined by visual inspection of the graphed residuals.

For the female mate preference trials, 18 females were presented with two males and mating occurred in 12/51 trials. Females showed no deviation from random mating with respect to male length or mass (Table 1) in the successful trials. Several females of large linear size did vigorously chase after mates with their chelicerae spread once mating ended. Cannibalism occurred in two trials in which two such females, who had indicated

Table 1.—Body characteristics and mate preference (binomial test, where $p = q = 0.5$).

Male mate preference			
Female characteristics		Mated females (<i>n</i>)	<i>P</i>
All trials			
Mass:	Heavier	45	0.0002
	Lighter	14	
Linear Size:	Larger	43*	<0.0001
	Smaller	13	
Body Condition:	Higher	42	0.0005
	Lower	17	
Trials in which mass differed by <20%			
Mass:	Heavier	10	0.176
	Lighter	9	
Linear Size:	Larger	5	0.0327
	Smaller	13	
Body Condition:	Higher	12	0.0328
	Lower	7	
Female mate preference			
Male characteristics		Mated Males (<i>n</i>)	<i>P</i>
Mass	Heavier	5	0.22
	Lighter	3	
Linear Size:	Larger	8	0.12
	Smaller	4	

sexual receptivity, consumed their mates immediately following mating and cheliceral disengagement.

Oviposition.—Of the 26 females used in the study of egg mass, 18 laid egg sacs for a total of 52 sacs. These 18 females laid between one and seven egg sacs ($\bar{x} = 2.7 \pm 0.4$ sacs). The egg sacs did not change significantly in volume as a function of whether they were the first ($\bar{x} = 0.051 \pm 0.009$ cm³), second ($\bar{x} = 0.031 \pm 0.006$ cm³); third ($\bar{x} = 0.026 \pm 0.004$ cm³) or fourth ($\bar{x} = 0.048 \pm 0.031$ cm³) sacs measured (first-second, unpaired t-test, $t = 1.124$, $df = 25$, $P = 0.27$; second-third, paired t-test $t = -0.50$, $df = 7$, $P = 0.63$; third-fourth, paired t-test, $t = -.99$, $df = 2$, $P = 0.42$). The number of days between the first and second egg sacs ($\bar{x} = 10 \pm 1.2$; $n = 15$, range 4–20 days), compared to the number of days between the second and third sacs ($\bar{x} = 7 \pm 1$; $n = 8$, range 2–10 days), did not significantly differ (unpaired t; $t = 1.81$, $df = 21$, $P = 0.084$). We were not able to test the

Table 2.—Regression of parameters of fecundity on female characteristics.

Female characteristic	<i>n</i>	<i>r</i> ²	<i>P</i>
Volume of first egg cluster			
Mass (day prior)	17	0.270	0.032
Linear Size	17	0.005	0.79
Body Condition	17	0.231	0.051
Summed volume of first and second egg clusters			
Mass (day prior)	15	0.278	0.003
Linear Size	15	0.018	0.48
Body Condition	15	0.321	0.0011
Summed volume of all egg clusters			
Mass (day prior)	17	0.119	0.18
Linear Size	17	0.001	0.89
Body Condition	17	0.205	0.068
Number of egg cases (two or more) produced			
Mass (initial)	15	0.079	0.31
Linear Size	15	0.024	0.58
Body Condition	15	0.058	0.39
Total number of egg cases produced			
Mass (initial)	18	0.048	0.38
Linear Size	18	0.052	0.36
Body Condition	18	0.025	0.53
Days to oviposition			
Mass (initial)	18	0.187	0.073
Linear Size	18	0.136	0.13
Body Condition	18	0.015	0.63

differences with the number of days between the third and fourth sacs ($\bar{x} = 9 \pm 6$; $n = 4$, range 5–17 days) and the number of days in between the fifth, sixth and seventh egg sacs (range 3–6 days) because the small sample sizes precluded any further analyses.

We used simple linear regression to examine the relationship between measures of the female body (mass, BCS and linear size) and measures of her fecundity, the volume of the egg cluster laid and the number of egg sacs produced (Table 2). Egg cluster volume was associated with female mass and BCS, while linear size was not. Significant relationships were found between female mass (prior to egg-laying) and the volume of the first egg cluster laid, as well as the summed volume of the first two egg clusters. Significant relationships were also found between female BCS and the summed volume of the first two egg clusters. Female linear size was not significantly associated with any measures of the volume of the egg clusters. Neither female

Table 3.—Female body characteristics on days prior and post oviposition.

Female characteristic	$\bar{x} \pm \text{SE prior}$	$\bar{x} \pm \text{SE post}$	<i>n</i>	<i>F</i>	<i>P</i>
Mass (1 d prior: 1 d post)	0.073 \pm 0.006	0.046 \pm 0.003	21	16.7	0.0002
Mass (1 d prior: 4 d prior)	0.059 \pm 0.005	0.051 \pm 0.004	16	1.62	0.21
BCS (1 d prior: 1 d post)	0.226 \pm 0.039	−0.226 \pm 0.062	21	38.1	<0.0001
BCS (1 d prior: 4 d prior)	0.179 \pm 0.053	−0.179 \pm 0.044	16	5.22	0.0295

Linear Size (No comparison: does not change in individual adult spiders).

mass, linear size nor BCS were associated with the total number of egg sacs produced.

Simple linear regression did not detect a significant relationship between mass, BCS or linear size and days to oviposition (Table 2). However, BCS and mass were significantly higher for females the day prior to oviposition than for females the day after oviposition (Table 3). BCS were significantly higher for females one versus four days prior to oviposition as well, yet this relationship was not seen with female mass (Table 3). We did not test linear size against the timing of oviposition, since an individual spider's linear size remains constant after its final molt as well as pre- and post-oviposition.

DISCUSSION

We examined three parameters of the female physique for their effect on male choice: mass, linear size, and body condition. Males overwhelmingly chose females who were heavier, longer, and had higher BCS. However, these three parameters were correlated, making it difficult to isolate the parameter(s) determining male choice. By looking at a subset of trials in which variation in female mass was partly controlled (less than 20% difference), we were able to separate linear size from the other two parameters. With the influence of mass minimized, males exhibited a significant preference for females with higher BCS, who *ipso facto* were the smaller females in these trials. Thus, we have shown that male choice is influenced by body condition, independent of mass and linear size. Our data set does not allow us to test mass in a similar fashion. Mass may have a similar independent effect on male choice, or it may merely be correlated with body condition. Female linear size, however, does not appear to influence male choice: it is merely correlated with mass and body condition.

Possible explanations for male preferences

are that they result in mating with females (1) carrying heavier egg loads, or (2) closer to oviposition. It is possible that male preferences could be influenced by other components of fitness such as increased egg size (but see Anderson 1990) or higher genetic quality, but these were not tested in this study. And we note that these hypotheses are not mutually exclusive.

The first hypothesis, that male preferences are influenced by egg load, has some support from our data. Female mass explained 12–28% of the variation in egg cluster volume, an estimate of egg load. Female body condition explains 21–32% of this variation. It appears that female mass and/or body condition may account for variation in the egg load a female is currently maturing but does not entirely predict her future success. Neither female mass nor body condition predicts the number of future egg sacs. However, variation in body condition explained 21% of variation in the summed volume of future egg sacs in our study. Several authors have reported relationships within orb-weaving species between increased female mass and increased egg load in spiders (Wise 1975, 1979; Morse 1988) and comparative studies across many species reveal selection for increased female linear size through fecundity selection (Head 1995; Prenter et al. 1999). Glazier (2000) reports positive associations between body condition and brood mass in amphipods, but we are not aware of any empirical evidence that body condition is positively associated with egg load in spiders.

The second hypothesis, that male preferences are influenced by proximity to oviposition, is somewhat supported by our data. Females do have significantly higher mass and body condition indices on the day of oviposition than at other times (the day after or 4 days prior). While the trend appeared to be in

the expected direction, we were unable to detect a significant relationship between female mass or body condition and overall time to oviposition. A partial explanation for this result may be that females gain mass rapidly just prior to oviposition. In *T. elongata*, the day before oviposition, females can gain weight in excess of 30% of their total body mass, all in one 24 hour period. As female spiders gain weight before oviposition, their abdomens swell with mature eggs. In an interesting twist, Funk and Tallamy (2000) found that females of the long-tailed dance fly deceive mate-seeking males with an unreliable signal that eggs are nearing maturation by inflating their abdomens (via swallowing air) in order to gain a protein meal in exchange for copulation.

Future studies to separate the effects of mass and body condition would be most helpful here. Several have argued that body condition is a better measure of fitness than mass (e.g., Jakob et al 1996; Glazier 2000), but data linking body condition to oviposition in spiders have yet to be reported. Both mass and body condition correlate with some measures of fecundity in our study, but our data set does not allow us to separate the effects of mass from those of body condition. The two parameters may be complementary.

In contrast to BCS and mass, we found no evidence of male preference for longer females, nor any relationship between female linear size and any parameters of fecundity or oviposition. There are several possible explanations for the lack of male response to longer females: (1) under lab conditions longer females are not much heavier than gravid small females, (2) female-female competition for high quality web sites favors longer females and leads to better foraging, and (3) mass is easier than linear size for males to assess from the edge of an orb web. These are discussed in turn below.

That female linear size would not influence egg load or the number or volume of future egg sacs is contrary to other fecundity studies of spiders (Marshall & Gittleman 1994; Head 1995; Prenter et al. 1999). However, in a more natural setting, female linear size could be strongly associated with feeding and egg sac production in *T. elongata*. All spiders in our egg sac study were fed the same amount of food to allow for controlled comparisons. In

the field, longer females may build larger webs or use higher-quality web sites to capture more food than smaller females. Female spiders tend to be food-limited (Wise 1975, 1979) so increased energy intake may allow for larger egg sacs, shorter intervals between egg sacs or increased longevity resulting in more egg sacs. Spence et al. (1996) found no relationship between linear size and reproductive output in the nursery web spider *Dolomedes triton* (Walckenaer 1837) when food availability was low. However, when more food was available than actually consumed, the reproductive output of larger females was significantly greater than that of smaller females. In our study, the lack of an effect of linear size may result from longer females being food-limited by access to smaller prey (Tipulidae and *D. virilis*) than the females would catch naturally, such as damselflies (Zygoptera) and moths (Danielson-François, pers. obs.).

Longer females may be heavier in the field as the result of better foraging from high quality web sites. There is competition for these high quality web sites from other females who invade each other's webs in aggressive interactions (Smallwood 1993). Sometimes these interactions result in the web owner losing her web to the intruder, and occasionally in a spider being killed and cannibalized (Smallwood 1993). If longer females are more likely to win in aggressive encounters (Rubenstein 1987), greater linear size may increase female fitness by reducing the probability that she loses her web site (which would interrupt her feeding), or is killed before depositing her eggs. These fitness consequences would not be detected by our measurement of egg production under controlled laboratory conditions.

Mass may be easier to assess than linear size in orb-weaving spiders, which have notoriously poor vision yet are able to accurately assess the mass of objects in their webs via vibrations (Suter 1978; Foelix 1996). In assessing a potential mate from a distance (at the edge of a web), mass may simply have been easier for males to assess or a more relevant cue than length for mate quality. For *T. elongata*, mating is guaranteed once the female in her web orients to the male on the web edge and both open their chelicerae (at a distance of 10 cm or more) and the male

speedily approaches to lock her chelicerae open. By the time both parties are within their range of vision, the decision to mate is a *fait accompli*.

We detected no clear patterns to female choice, but a high proportion of trials, 39 out of 51, did not result in any mating. The resulting small sample size may have prevented us from detecting any female preferences. It is also possible that the simultaneous proximity of two males disrupted the normal behaviors of the female as a fair number deserted their webs. It was rare for us to observe more than one male interacting with a female or her web in the field. Alternatively, male-male competition for access to females might normally prevent females from encountering a range of male linear sizes. Two of us (ADF, PDS) have seen direct evidence of male-male competition in the field: two males fighting directly adjacent to a female's web. The winner of the contest mated with the female immediately afterwards. Future experiments to determine whether the female is actually choosing or merely accepting winners are needed. Female preference may be difficult to detect because females may be choosing males post-mating via cryptic female choice (Eberhard 1994, 1996). Cannibalism may be the end result of a female preference, yet it was an infrequent occurrence (occurred in two mating trials). While our limited data support that smaller males are more likely to be cannibalized (Elgar & Nash 1988), female hunger level may be a better predictor (Andrade 1996).

The mating history of males and females was unknown because they were collected as adults. Our study assumes that the mating history of females was random relative to female length and mass so our conclusions regarding male choice should hold. In this species, past mating history may not have as significant influence on male mate choice as expected for most spiders because female *T. elongata* are predicted to have last-male sperm precedence, continually deposit egg sacs at regular intervals and continue to be receptive to further mating.

As far as we know, this is the first report of body condition influencing mate choice in spiders. Taylor et al. (2000) suggest that the display used by the salticid *Plexippus paykulli* (Audouin 1826) is designed to convey infor-

mation about body condition to potential mates and rivals. Salticids are known for their visual acuity. It is not clear how male *T. elongata* would sense body condition in nearby females unless length and mass are separate components of a vibratory signal transmitted through the web. It may be that there is some other signal (e.g., pheromone) that correlates with an important parameter of female fecundity, which is also correlated with body condition.

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POPULATION DYNAMICS OF TWO SPECIES OF KLEPTOPARASITIC SPIDERS UNDER DIFFERENT HOST AVAILABILITIES

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ABSTRACT. Kleptoparasitic spiders are known to have a close association with host spiders, yet there have been few studies demonstrating how host availability influences the dynamics of kleptoparasites. Field surveys were conducted at five sites differing in host composition in sub-tropical areas in Japan, at about two-months intervals. *Argyrodes flavescens* and *A. bonadea* were both found more frequently on webs of two *Nephila* species than expected from the web areas they occupied among webs of all web spiders. Seasonal dynamics of *Argyrodes* changed greatly according to whether *N. clavata* was present or not, indicating the importance of *Nephila* on *Argyrodes* populations. The peak density of *A. bonadea* came earlier than that of *A. flavescens*. Because *A. flavescens* is known to limit the number of *A. bonadea* on host webs, the decrease in the density of *A. bonadea* may be due to the effect of interspecific competition by *A. flavescens*.

Keywords: Interspecific competition, parasite, Theridiidae, phenology

Spiders in the genus *Argyrodes* Simon 1864 are often called kleptoparasites that rely almost exclusively on host spiders. However, the interaction between *Argyrodes* and their hosts is complex: *Argyrodes* can be kleptoparasites, commensals, or predators to their hosts depending on the species and host conditions (e.g., Trail 1980; Tanaka 1984; Larcher & Wise 1985; Whitehouse 1986; Cangialosi 1997). These close associations lead to the inference that population dynamics of *Argyrodes* is highly dependent on host availability. Vollrath (1987) demonstrated the dynamics of two *Argyrodes* species and their host *Nephila clavipes* (Linnaeus 1767). However, there have been no studies showing how changes in host species composition influences *Argyrodes* dynamics. Ideally such a causal relationship should be evaluated by field experiments in which a particular host is removed, but population manipulation on a large scale sufficient to change host availability is impractical. Examining the variation of kleptoparasite dynamics in areas differing in host availability seems to be the only way to estimate the strength of associations between the host and kleptoparasite at the population level.

On Okinawa Island located in the southwestern part of Japan, two *Argyrodes* species,

A. flavescens O. Pickard-Cambridge 1880 and *A. bonadea* (Karsch 1881), are commonly found on orb-webs of various spider species. Preliminary observations revealed that a large number of the two species was found on the webs of *Nephila clavata* and *N. maculata* (Fabricius 1793). These two *Nephila* species have different phenologies, the former emerging later in the season. Also, the distributions of the two species differ, *N. maculata* lives all over the island while *N. clavata* inhabits only the northern part of the island. These characteristics enable us to estimate the importance of host availability.

In this paper I examined seasonal dynamics of the two *Argyrodes* species and their potential host spiders in five sites differing in host species compositions. I hypothesize that 1) the *Nephila* species are the preferred host for *Argyrodes*, and 2) the presence or absence of *Nephila clavata* changes population dynamics of *Argyrodes* greatly.

METHODS

Field studies were conducted at four sites on Okinawa Island, Nakagusuku (NK), Nangusuku (NG), Shoshi (SH), Nakijingusuku (NJ), and at one site on Iheya Island (IH), southwestern Japan. The climate of these sites

is sub-tropical, with an average temperature of 22.6 °C and an annual rainfall of 2,100 mm. Previous observations revealed that *Nephila clavata*, a major host for *Argyroides*, lives at all sites except for NK which is located at the southern part of Okinawa Island. Iheya Island lies about 60 km away from Okinawa Island and is much smaller (about 20 km²) than that of Okinawa Island (about 1,199 km²). Thus I expected densities and/or species richness of host spiders to be low on that island.

I established two 50 m lines along the roadside in forests at each site, and surveyed these transects five times (four times for IH) from July 1997 to April 1998 at intervals of approximately 2–3 mo. I recorded all web spiders with body lengths larger than 4 mm living within 2 m from the transect and 2 m from the ground. I recorded the spider body length, the vertical and horizontal web diameters, any prey being consumed, and any small insects remaining in the web. At the same time I counted and recorded the body length of all *Argyroides* found on the spider webs with calipers. Because it was difficult to know the stage of *Argyroides* in the field, I used body length as an indicator for the stage and determined the smallest size of adults, viz., 3 mm for *A. flavescens* and 2.5 mm for *A. bonadea*.

In this study, web areas of hosts instead of density of host individuals was used for representing host availability because the body size of host spiders varies greatly depending on the species and seasons. For instance, the web of *Nephila maculata* is much larger than that of most other spiders, so that the amount of habitat and food resources available to *Argyroides* may vary greatly.

The density of each *Argyroides* on a particular host species (no./cm²) was calculated as follows, $\sum N_i / \sum A_i$, where N_i is the number of *Argyroides* on the i^{th} web of a particular host species and A_i is the web area of the i^{th} web. Data from the two transects were combined at each site. A binomial test was performed to ascertain whether each *Argyroides* prefers a particular host spider species. The null hypothesis was that the total number of *Argyroides* on webs of host species j (N_j) is determined by the proportion of the web area of that host, i.e.,

$$N_j = A_j / \sum A_j \cdot \sum N_j,$$

where A_j is the total web area of host species

j and N_j is the total number of *Argyroides* sp. on host species j . Hosts harboring at least ten *Argyroides* or those occupying more than 30% of the total web areas of all species combined were used for the analysis. Significance level was adjusted by the sequential Bonferroni method (Sokal and Rohlf 1995) for each season.

RESULTS

Dynamics of *Argyroides* and their host.—

The kleptoparasitic spiders found in this survey were mostly *A. flavescens* and *A. bonadea*. Figure 1 shows seasonal changes in the density of the two *Argyroides* spp. and web areas of host spiders in five study sites. In NK where *N. clavata* is absent, the dynamics of web area were mostly determined by *N. maculata*. Although the peak density of *A. flavescens* was delayed relative to that of host web area, its density decreased abruptly in November when *N. maculata* disappeared. In NG, SH and NK, however, *N. clavata* is abundant in November, and *Argyroides* maintained high densities in November. It is noteworthy that the timing of peak density of the two *Argyroides* species differed, with *A. bonadea* reaching the peak earlier. Another important point is that both *Argyroides* densities declined to low levels in January and April when web areas of spiders other than *Nephila* remained at levels similar to those in November. The main species in this period were *Leucauge blanda* (L. Koch 1878), *Cyclosa confusa* Bosenberg & Strand 1906 and *Neoscona scylla* (Karsch 1879). In IH where *N. clavata* was not found on the census route, the density of *Argyroides* showed a peak in August and then dropped sharply in November, which is similar to the situation in NK. Unlike other study sites, the density of *A. bonadea* was much higher than that of *A. flavescens*.

Percentage of adult *Argyroides*.—The percentage of adult individuals was calculated separately for areas where both *Nephila* species were present (NG, SH, NJ) and *Nephila clavata* was absent (NK, IH). In areas where both *Nephila* species were present, seasonal change in the percentage of adults differed greatly between the two *Argyroides* (Fig. 2). The peak occurrence of adult *A. flavescens* was found in autumn while that of *A. bonadea* was in spring and early summer. In areas where *Nephila clavata* was absent, the differ-

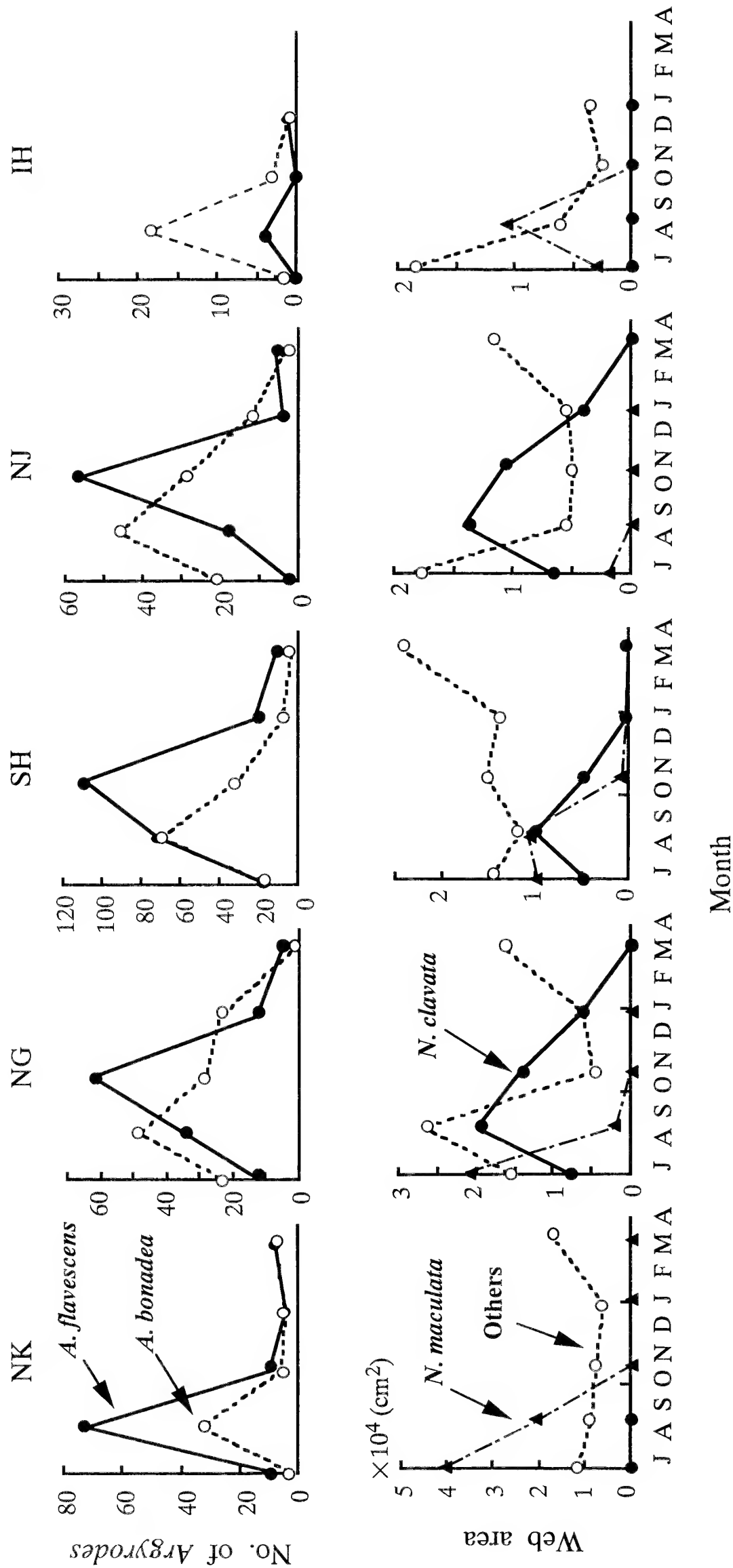


Figure 1.—Seasonal dynamics of the numbers of the two *Argyrodes* species, and web areas of the two *Nephila* species and other web spiders in 5 sites in Okinawa.

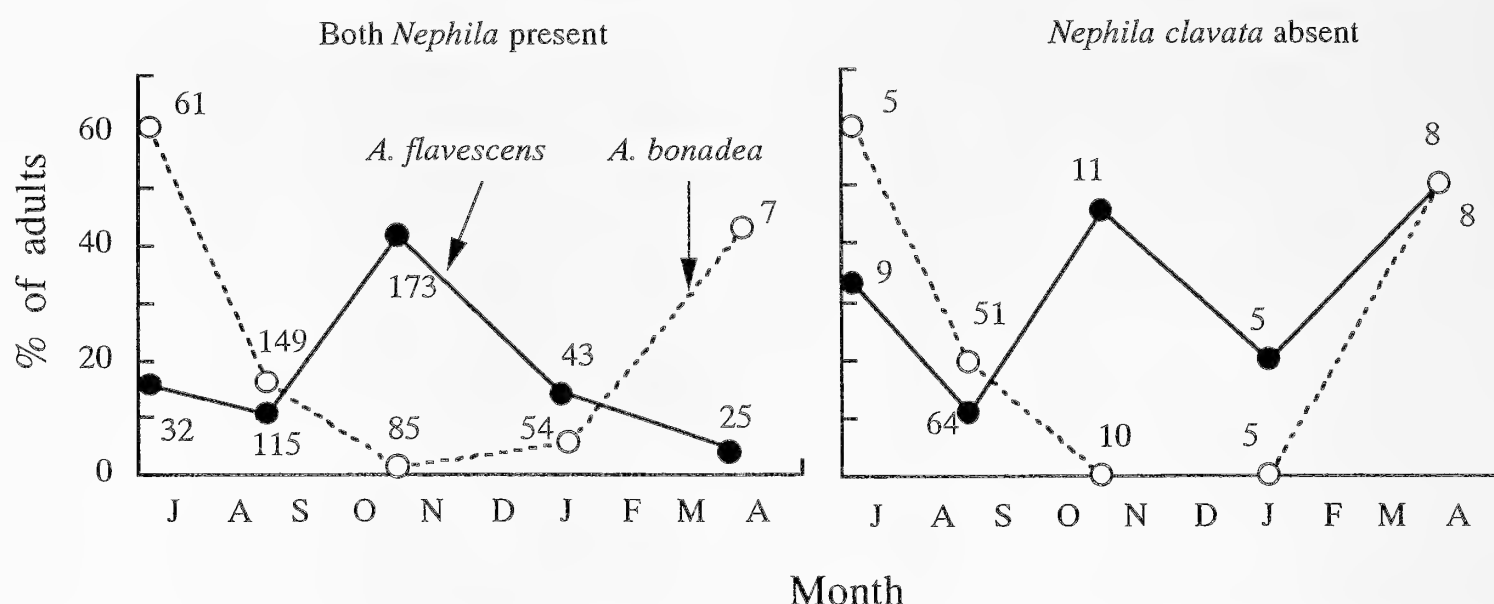


Figure 2.—Percentage of adult *Argyrodes* in areas with and without *Nephila clavata*. Numerals in the figure represent sample size.

ence was less conspicuous due to the high percentage of adult *A. flavescens* in spring. *Argyrodes bonadea* showed a similar seasonal pattern in the two types of areas.

Host preference of *Argyrodes*.—A total of 18 species of web spiders was recorded including all sites and seasons (Table 1). Twelve species were found to be hosts for *A. flavescens*, and 14 were hosts for *A. bonadea*.

The results of the binomial tests (Table 2) revealed that *A. flavescens* had a strong tendency to prefer *Nephila clavata* in August and November, although no preference was found in July when *Nephila clavata* was still small in body size. *Nephila maculata* was preferred in July probably because *Nephila* was already large. Besides the two *Nephila* species, only *Argiope minuta* was preferred significantly. *Leucauge blanda* and *Cyclosa confusa* had significantly fewer *A. flavescens* on their webs than expected from their web areas.

Argyrodes bonadea also preferred *N. clavata* in August and November, but the preference for *N. maculata* was obscure. Unlike *A. flavescens*, *Cyrtophora moluccensis*, which builds large, horizontal and tightly-meshed webs, was a preferred host for *A. bonadea*. *Leucauge blanda* had fewer *A. bonadea* than expected from its web area.

Prey density on host webs.—Figure 3 shows seasonal changes in prey density on *Nephila* webs. In all areas, prey density on host webs increased in November and then decreased markedly in January. The main prey

in November were small plant hoppers in all study sites.

DISCUSSION

The dynamics of the two *Argyrodes* species were largely affected by the phenologies of *Nephila* species. This is clearly illustrated by the following findings: 1) where there is no *N. clavata* (NK and IH), densities of *Argyrodes* declined rapidly in November when *N. maculata* had disappeared; but where both *Nephila* species were present, the density increased in November for *A. flavescens* and decreased slightly for *A. bonadea*; 2) preference for *Nephila* webs was prominent, especially by *A. flavescens*. The first finding is particularly good evidence for the importance of *Nephila* on *Argyrodes* dynamics because this can be viewed as a “natural experiment” in which one major host was “removed”. Grostal & Walter (1999) revealed a similar result showing that *Nephila* spp. were the preferred hosts for *A. antipodanus*. The reason why *Nephila* webs are suitable for *Argyrodes* may be that these webs have a barrier web on both sides of the capture web, providing a space for living. The significance of barrier webbing for *Argyrodes* has already been argued by several researchers (Whitehouse 1986 & 1997; Canigalosi 1997). Comparing the two *Nephila* species, *N. clavata* has a more elaborate barrier web and *N. maculata* sometimes lacks a barrier web (unpub. obs.). This may explain why *N. clavata* was preferred more frequently

Table 1.—Host spiders for the two *Argyroides* species found in the census route in each study site (all seasons pooled). (+) = *Argyroides* found, (–) = *Argyroides* not found, blank = host not found.

Site	Host species												
	Nm	Nc	Av	Ar	Cm	Cu	Gm	Lb	Ns	Nsu	Nt	Er	Cc
<i>Argyroides flavescens</i>													
NK	+		+				+	+	+	+			+
NG	+	+	+	–	–	–	–	+	+	+		–	+
SH	+	+	–		–		+	+	+	–	+		+
NJ	–	+	–		+		+	+	–	–			+
IH	+				–		–	–	–	–			+
<i>Argyroides bonadea</i>													
NK	+		+				+	+	–	+			+
NG	+	+	+	–	+	+	–	–	+	–		–	+
SH	+	+	–		–		+	+	+	–	+		+
NJ	+	+	+		+		+	+	+	+			–
IH	+				–		–	+	+	–			+

Nm = *Nephila maculata*, Ar = *Araneus* sp., Gm = *Gasteracantha mammosa*, Nsu = *Neoscona subpullata*, Cc = *Cyclosa confusa*, Am = *Argiope minuta*, Nc = *Nephila clavata*, Cm = *Cyrtophora moluccensis*, Lb = *Leucauge blanda*, Nt = *Neoscona theisi*, Cm = *Cyclosa mulmeinensis*, Te = *Tetragnatha* sp., Av = *Araneus ventricosus*, Cu = *Cyrtophora unicolor*, Nc = *Neoscona scylla*, Er = *Eriophora yanbaruensis*, Aa = *Argiope aemula*, and Ac = *Achaearanea* sp.

Table 2.—Results of binomial test to assess whether each *Argyroides* species prefers a particular host spider. The null hypothesis is that an *Argyroides* chooses a host spider in proportion to its web area. Positive signs mean preference (+++ = $p < 0.001$, ++ = $p < 0.01$, + = $p < 0.05$), negative signs mean avoidance (--- = $p < 0.001$, -- = $p < 0.01$, - = $p < 0.05$). Abbreviations for species name are the same as in Table 1.

Argyroides flavescens

Site	Month	Host species							
		<i>Nm</i>	<i>Nc</i>	<i>Av</i>	<i>Cm</i>	<i>Lb</i>	<i>Ns</i>	<i>Cc</i>	<i>Am</i>
NK	Aug	+++			ns			—	
NG	Jul	ns	ns				ns		
	Aug		+++	---					
	Nov		++	ns				ns	
SH	Jul	+++	ns			ns			ns
	Aug	ns	+++						ns
	Nov	ns	+++			---			++
NJ	Jul								
	Aug		ns					ns	+
	Nov		+++			—			
IH	Aug								

Argyroides bonadea

Site	Month	Host species							
		<i>Nm</i>	<i>Nc</i>	<i>Av</i>	<i>Cm</i>	<i>Lb</i>	<i>Ns</i>	<i>Cc</i>	<i>Am</i>
NK	Aug	++				—		ns	
NG	Jul	ns	ns				ns		
	Aug	ns	+++	--	ns				
	Nov		+	ns				ns	
SH	Jul	ns	ns			ns			
	Aug	---	++			—			+
	Nov	ns	ns			ns		ns	ns
NJ	Jul		ns	ns	+				
	Aug		+++		+				ns
	Nov		+			ns			
IH	Aug	ns						ns	

than *N. maculata* by the two *Argyroides*. Other studies have shown that *Argyroides* spiders often live in *Nephila* webs (e.g., Elgar 1993) but only a few of them have demonstrated the seasonal dynamics of *Nephila*-*Argyroides* systems. Vollrath (1987) showed that the dynamics of *A. elevatus* and *A. caudatus* were closely related to the number of *N. clavipes* in Panama, yet no evidence was provided showing that alternative host spiders were not responsible for this pattern. The present study clearly demonstrates the importance of *Nephila* as hosts for *Argyroides* both from the “natural experiment” and preference analysis.

Another interesting point in the population dynamics of the two *Argyroides* is that the peak density of *A. bonadea* was earlier than that of *A. flavescens*. This difference may be due to interspecific competition between the two *Argyroides* species. Miyashita (2001) demonstrated that experimental removal of *A. flavescens* increased number of *A. bonadea* within only 2 d, and the number of individuals removed was positively correlated with the rate of increase in *A. bonadea*. Although this experiment indicated interspecific competition on a small spatial scale, this effect is likely to extend up to regional scales. There is additional circumstantial evidence supporting the likelihood of interspecific competition. In a temperate area where only *A. bonadea* was present, Yasuda (pers. comm.) found that this species is most abundant in mid-October which is the late adult period of *N. clavata*

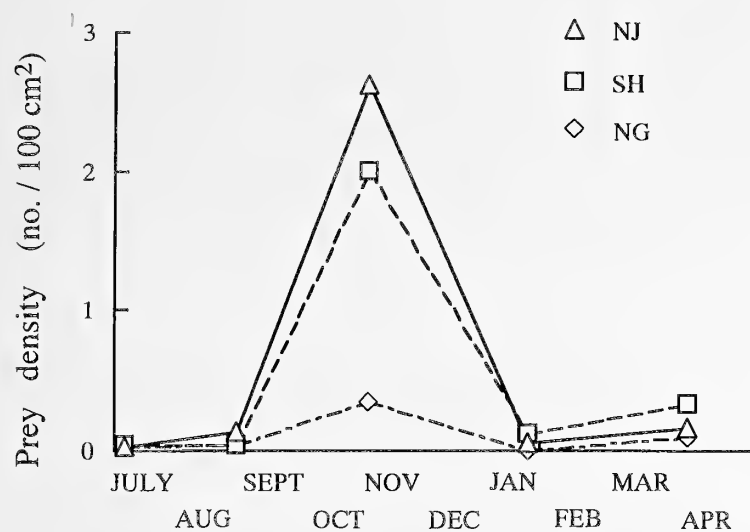


Figure 3.—Seasonal change in prey density (no./web area) on host spider webs. The 3 sites shown here have both of the two *Nephila* species.

and 2 mo behind the peak of the web area. On Okinawa, however, *A. bonadea* showed a peak in late August and the density decreased in November, the beginning of the adult period in Okinawa. This means that *A. bonadea* living in regions without *A. flavescens* showed host-parasite dynamics similar to *A. flavescens*. Accordingly, interspecific competition by *A. flavescens* may have shifted the dynamics of *A. bonadea* to earlier seasons. An alternative explanation is that the life cycle of *A. bonadea* in sub-tropical Okinawa is different from that of the temperate area, which is unrelated to competitive interactions with *A. flavescens*. It would be difficult to test whether there is a causal relationship between the dynamics of the two *Argyroides* species because large scale experimental manipulation is necessary.

Host composition appears to have a minor impact on the age structure of *Argyroides*, especially for *A. bonadea* (Fig. 2). The increase in the proportion of adults in spring in areas without *N. clavata* might have been an artifact due to the small sample size ($N = 8$). Adults of *A. flavescens* were found throughout the year but the peak was in autumn when prey on host webs were most abundant. If the increase in prey availability had already been initiated in October, this can explain the higher proportion of adults in November, because spiderlings of *A. flavescens* can reach maturity and produce egg sacs in a month (unpub. obs.). Contrarily, adults of *A. bonadea* were rarely found in autumn, suggesting *A. bonadea* does not accelerate its developmental rate

by consuming prey abundant on host webs but adjusts its life cycle by retarding its development. It appears that *A. flavescens* has a more opportunistic life cycle strategy than *A. bonadea*.

From winter to spring when the main hosts were absent, *Argyroides* spiders were found to live on the webs of smaller orb-weavers such as *Leucauge blanda*, *Cyclosa confusa* and *Gasteracantha mammosa*, which were not preferred in the presence of *Nephila*. Whitehouse (1988) found that the host range of *A. antipodiana* in winter was larger than that in growing and reproductive seasons, probably because overwintering individuals need webs for shelter only. However, the situation of *Argyroides* in the present study is quite different because I often observed *Argyroides* ingesting silk of host webs as well as stealing prey (unpub. obs.). The difference is mainly due to climate conditions: the present study was made in the sub-tropics whereas the study by Whitehouse was in a temperate region. Although it seems unlikely that sub-tropical *Argyroides* can obtain sufficient food in winter, they may be able to survive the harsh period by living on unfavorable hosts. Grostal & Walter (1999) found no *A. antipodanus* on webs of *Leucauge* sp. and *Gasteracantha* sp. in Australia but the season they studied was the period when the main host *Nephila* was present. It seems necessary to clarify the role of non-preferred host for the maintenance of *Argyroides* populations.

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LACK OF TASK DIFFERENTIATION DURING PREY CAPTURE IN THE GROUP LIVING SPIDER *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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ABSTRACT. *Stegodyphus mimosarum* of the African savanna form communal nests consisting of few to several hundred individuals and co-operate in nest construction and maintenance, brood care and prey capture. We tested large and small individuals for differential responses to different prey risk types. To date, there has been no conclusive evidence of tasking in these or other social spiders. If tasking occurs, small spiders should approach and attempt to subdue less dangerous prey items such as flies more often than the more dangerous prey items such as bees. Hungry individuals were significantly more willing to venture out of the nest refuge and thus accept the costs associated with prey capture than were satiated spiders. Apparent depletion of poison in previous prey captures did not significantly affect an individual's response to a prey item. Spiders treated more dangerous prey (bees) more carefully than less dangerous prey (flies), but there was no difference in the response of large versus small spiders to prey. The two-way interaction between spider size and prey type was never statistically significant, indicating a lack of tasking in this species.

Keywords: Foraging, co-operation, social, communal

Recent approaches to eusociality and co-operative breeding suggest that these two concepts should not be treated as discrete phenomena. Rather they should be viewed as points along a continuum uniting fundamentally similar social systems, whose main differences lie in the distribution of lifetime reproductive success among group members (Keller & Reeve 1994; Sherman et al. 1995). The social spiders may be best placed near the co-operative breeding end of the scale, in which many individuals in the colony may reproduce (Lubin 1995). Unlike social insects, no co-operative breeding spiders studied to date have shown evidence of either ethological or morphological caste systems (Tietjen 1984; Ward & Enders 1985; Lubin 1995; but see Rypstra 1993). Nevertheless, there are several activities within the spider communities which may be subject to division of labor. These include prey capture (the focus of this

paper), brood care, web-building and nest maintenance. Task specialization could increase the overall efficiency of performance of these activities, thereby increasing colony success (Oster & Wilson 1978; Lubin 1995).

Stegodyphus mimosarum Pavesi 1883 are social spiders which inhabit dry African savanna. They form communal nests containing few to several hundred individuals which co-operate in nest construction and maintenance, prey capture and brood care (Seibt & Wickler 1988). A great variety of prey is captured in the field ranging from small flies to large grasshoppers (Ward & Enders 1984; pers. obs.). By leaving their refuge (nest) in order to approach a prey item, spiders become vulnerable to predators and parasites and also run the risk of becoming injured by large prey.

Given individual variation in size there may be differential effectiveness at prey capture. Under such circumstances it may be advan-

tageous for tasking among individuals, with each individual allocating its resources to the most effective use. Furthermore, we expect tasking to evolve under either an individual selection or group (kin) selection argument. We tested the hypothesis that prey capture is subject to task differentiation, with tasks determined by spider size in relation to danger (handling difficulty) posed by the prey. We predicted that larger spiders would approach more dangerous prey, while small individuals would avoid large prey in favor of smaller, less dangerous prey items. Note that the range of prey items used in this experiment was well within a size that more than one colony member would share in feeding. Only very small items are eaten by single spiders. Note also that not all individuals feed on every prey item.

The test that we provided may be confounded by two factors: (1) motivation differences due to time since previous feeding; and (2) depletion of poison from previous capture attempts. We tested whether these may be confounding factors by separate experiments using a similar design.

Only juvenile female spiders were used in this study. Eight active *S. mimosarum* nests were removed during March and April 1997 from the Weenen (28°50'S; 29°40'E) and Itala (31°13'E; 27°31'S) Game Reserves in KwaZulu-Natal. They were held in the animal house at the University of Natal (Durban). The nest is usually built around a central branch which functions as a support for the entire structure. These colonies were divided into smaller colonies using individuals from the same original nest, and placed in glass jars together with small *Acacia* branches. The number of spiders in the colony was determined for each experiment. The colonies were then left for about 7 days to provide time to settle into a colony and construct a retreat and capture web. The experiments were performed indoors under daylight conditions, and spiders were housed in rooms with windows allowing natural light cycles. During the task experiment (see below) a desk lamp was placed near the colonies to increase spider responsiveness. The lamp was turned on 0.5 h before observations, and turned off after observations (all experimental groups treated equally). The experiments were carried out from May–September 1997.

The colony sizes that we established were relatively small at 4–6 spiders (see below). Although *S. mimosarum* colonies can range up to several hundred individuals, it is common to find nests of fewer than 10 spiders. This is particularly so at colony foundation. Examining the payoffs of individual strategies in small group size is the essence of the study of the evolution and maintenance of sociality. We believe that although the colony sizes chosen for this study are at the small end of the size distribution, they do reflect natural circumstances, and particularly, reflect critical colony sizes in terms of individual selection of strategies.

Effect of hunger on spider response.—Ten spider colonies, each consisting of six spiders, were established. Spiders were marked on the abdomen using paint-pens, with individuals in a colony receiving the same color. Five colonies were presented with a house fly *Musca domestica* on a daily basis for a period of 3 days. The other five colonies remained without food for 7–14 days prior to commencing the experiment.

Colonies consisting of 8 spiders were used to construct pre-existing webs for the experiment. Once web construction was complete, these spiders were removed. This was done to ensure that both the hungry and the satiated spiders were equally unfamiliar with the web into which the prey item was placed. Spiders which construct their own capture web are expected to be more familiar with the architecture of the web and therefore more capable of directly approaching the prey item (Downes 1994).

Three spiders from each colony were then placed into a glass jar containing a pre-existing web. A house fly was then placed in each capture web. A house fly was used as the prey item so as to exclude the possible influence of danger on the spider's response. The individual which approached the prey first and the amount of time taken before the first spider reached and bit the prey item was recorded.

Mann-Whitney U-tests were used to detect significant differences in the approach time between satiated and hungry spiders. Each colony was an independent sample with the fastest spider to emerge of the 3 hungry spiders and the fastest to emerge of the three satiated spiders being used for each colony. G-tests were used to determine significant differences

in the number of responses from hungry and satiated spiders. The counts were tested against a 50:50 expectation.

Effect of prior capture attempt on spider response.—Eight colonies, each with four individually marked spiders, were established in glass jars as described earlier. A house fly was placed in the capture web and the subsequent events were recorded. We noted which spider was the first to bite the prey and the time at which this occurred. The spiders were left to bite, and presumably inject venom and enzymes, until the first spider had been biting for a time period of not less than five min but not exceeding 15 min. Spiders were allowed sufficient time to inject the prey with venom and enzymes but not to feed. This is based on observations of another social species, *S. dumicola* Pocock, 1898, where there was little or no mass gain by spiders during the first 20–30 minutes of “feeding” (Whitehouse & Lubin 1999; Amir et al. 2000).

After the designated time period, the prey item was removed. The colony was immediately presented with another prey item and subsequent spider behavior was recorded and timed. This was repeated a third time with a third prey item. Immediate presentation of the second and third prey items was necessary in order to limit the amount of time that the spider had to recover from the previous attack and to replenish its venom supply. The identities of the individuals that bit the first, second, and third prey items were noted to determine whether the spider that approached the second or third prey item was the same individual that approached the first prey item. If venom and enzyme availability affects a spider’s readiness to approach and attempt to subdue prey, or if there is physical or sensory fatigue or adaptation, the individuals that had previously attacked the prey would be unlikely to approach subsequent prey.

Spiders’ responses were classified into two groups: (1) spiders that approached more than one prey item and were assumed to show no venom depletion or fatigue; and (2) spiders that approached only a single prey item and in which depletion or fatigue may have occurred. These data were analyzed using a G-test (with William’s correction) on the counts of these two classes.

Task differentiation in *S. mimosarum*.—Sixteen independent colonies were estab-

lished, with the experiment run as two sets of eight colonies. Each colony consisted of two large and two small individuals, and each spider in each colony was marked using a paintbrush. The first set of replicates was carried out from 6 June–14 July 1997, while the second set of replicates was carried out from 17 June–15 September 1997. Each colony was presented with each prey type three times with the median response to these being used as the measure of the response of that colony to that prey type. This served to increase the internal validity of the results without pseudoreplication affecting the power of the test because each colony was represented once for a response for each spider size to each prey type.

Each colony was randomly presented with two different prey items which represented different degrees of danger. Less dangerous prey was represented by a housefly, and more dangerous prey was represented by a honey bee *Apis mellifera*. Prey items were presented either every 24 h or every 48 h, depending on the amount of capture web present. On several occasions, previous prey captures had resulted in extensive web damage and thus the colonies were not fed until the web was sufficiently repaired. This occurred within 2–7 days after the previous prey capture. Because we combined responses using the median of three replicates prior to analysis, such variation in prey presentation would not bias the data. Each colony was observed from the time of prey presentation until the prey had been subdued to the point at which the prey item could no longer move or escape from the spiders. Spider behavior was assigned to the following categories: (1) spider approached the prey. This behavior included any movement spiders made towards the prey. (2) Spider made contact with and held onto the prey. This behavior was allocated to the spider each time the spider touched or held on to the prey item, but did not actually bite the prey item. (3) Spider made contact with the prey and bit it. (4) Spider retreated. This behavior included any movement of the spider away from the prey item.

In some cases involving honey bees, major web destruction by the bees resulted in them being able to escape. In these cases, bees were immediately placed back into the capture web and timing resumed. If, however, a bee managed to escape more than five times within

half an hour, the experiment was terminated and repeated at a later date. The amount of time the prey item took to escape ranged between 7–90 min depending on the size of the capture web the spiders had constructed. This time period was sufficient to enable us to ascertain which spiders approached more frequently, and which spiders made contact with the prey.

The results of these experiments were analyzed using a two-factor analysis of variance (ANOVA) with an interaction term. This term represents the interaction between spider size and prey type, and is critical in interpreting whether task differentiation occurred. A significant interaction term indicates task differentiation, as it suggests that large and small individuals respond differently to the two prey types. We analyzed seven independent variables using ANOVA: (1) handling time that was the sum of the mean amount of time which a spider spent approaching, holding and biting the prey item. This variable was analyzed first, as it represented the most likely variable to reveal task differentiation in these colonies. (2) The mean number of times small and large spiders approached the prey item. (3) The mean number of times small and large spiders bit the prey item. (4) The mean time large and small spiders spent in contact with the prey item. (5) The mean time spiders spent biting the prey. The final two variables related to the reluctance of the spiders to approach a prey item. These included: (6) the mean number of retreats; and (7) the mean amount of time spent retreating from and not approaching the prey item. The independent factors included in the ANOVA were prey type (bee and fly) and the spider size (large and small), with an interaction term.

Given that we analyzed the same data set seven times, we performed a Bonferroni adjustment to the data (Schork & Remington 2000). In this case we changed the critical *p*-value for rejection of the Null Hypothesis from 0.05 to 0.007 (0.05/7).

RESULTS

Effect of hunger on spider response.—

The degree of satiation did affect a spider's willingness to approach and attempt to subdue a prey item (G-test: $G_{adj} = 5.44$, $df = 1$, $P < 0.05$). Hungry spiders were significantly more likely to approach a prey item than sa-

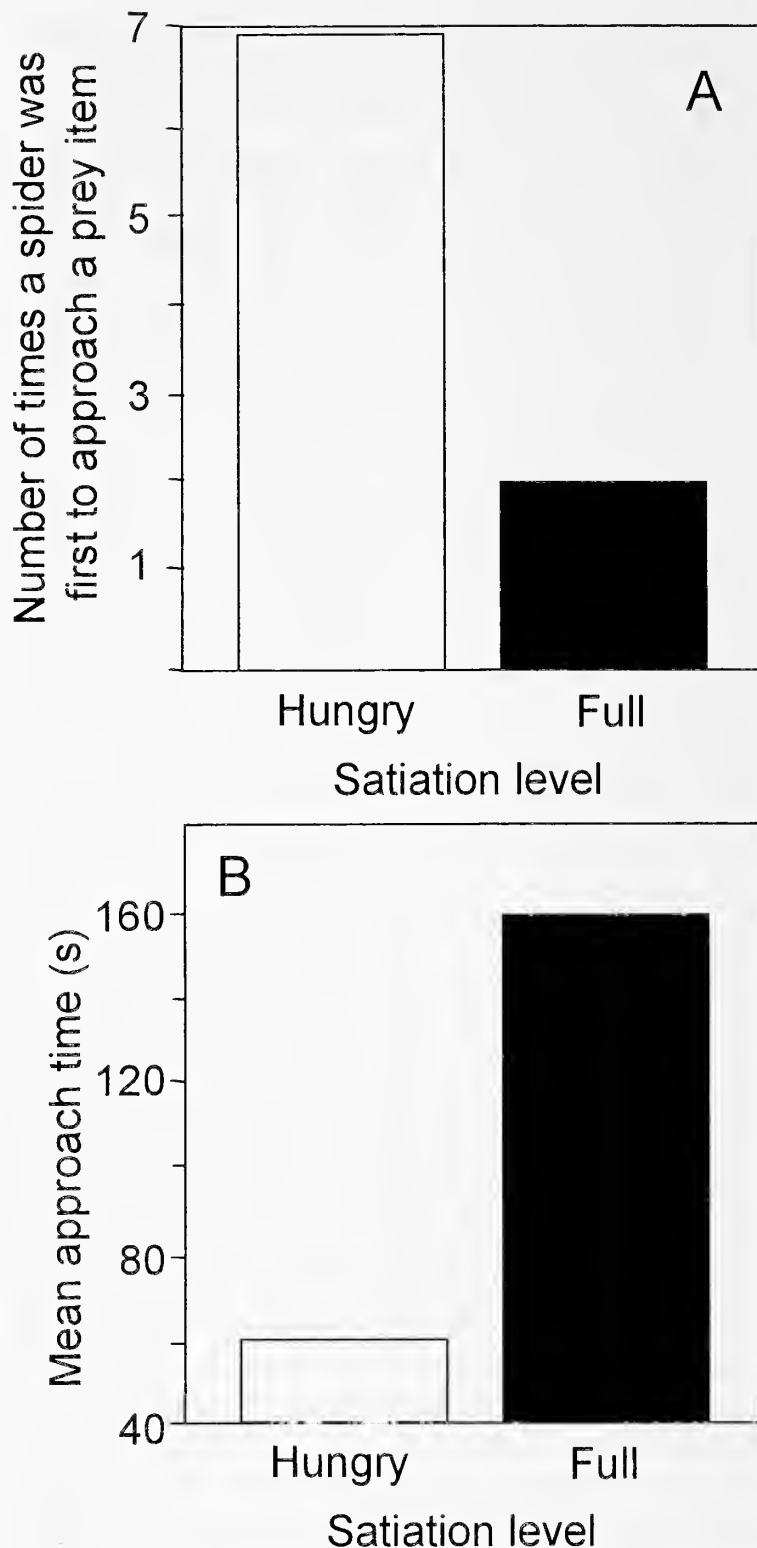


Figure 1.—Effect of satiation level on response of spiders to house flies placed in their webs. (A) First approach to prey item by either category and (B) mean time to approach of unfed (hungry = open bars) and fed (full = closed bars) spiders. $n = 9$ colonies.

tiated spiders and therefore this factor is important in driving the prey capture process (Fig. 1A). Hungry spiders responded faster to the prey item than satiated spiders. The mean approach time for satiated spiders was 159 sec (range: 60–258) while the mean approach time for the hungry spiders was 60 sec (range: 8–88) (Mann Whitney-U test; $Z = -1.84$, $n = 9$, 1-tailed $P = 0.03$) (Fig. 1B).

Effect of prior capture attempt on spider

response.—Given that there were four spiders in each colony, we expected each individual to come out 25% of the time. When comparing the second prey item to the first, in 2/8 (25%) colonies it was the same spider responding to both prey items. When comparing the third prey item to the second prey item, in 3/8 (38%) colonies it was the same spider responding to both prey. Spiders do not appear to alternate in approaching consecutive prey items ($G_{adj} = 2.18$, $df = 1$, $P > 0.05$). This suggests that enzyme or venom depletion did not occur, nor did spiders show fatigue or sensory adaptation.

Task differentiation in social spiders.—Using the more conservative statistical interpretation analysis (for all values above $P = 0.007$, the Null Hypothesis of no difference was accepted), only three dependent variables showed significant main effects. In all cases there was a significant Prey Type effect on handling time (Fig. 2) (a combined variable indicating time approaching, in contact with, and biting the prey item), mean number of contacts (Fig. 3A), and mean number of retreats (Fig. 4). Spiders spent significantly more time handling, had significantly more contacts with, and showed significantly more retreats from the dangerous bee than the less dangerous fly. These results were not effected by spider size (main effect spider size $P > 0.007$ in all cases).

However, there was one analysis where spider size was marginally not significant. There was a trend for large spiders to bite more often (regardless of prey type). We have interpreted this as not statistically significant based on a Bonferroni adjusted critical p-value. However, under a conventional analysis with P -critical (α) = 0.05, this result would be interpreted as statistically significant.

In all of the above tests, the two-way interaction between spider size and prey type was not statistically significant ($P > 0.007$ in all cases). Thus, spiders did not modify their behavior toward different prey types in accordance with their body size differences.

DISCUSSION

The degree of hunger experienced by the spider determined the spider's willingness to approach prey. Hungry spiders responded significantly more often and approached the prey more quickly than satiated spiders. The degree

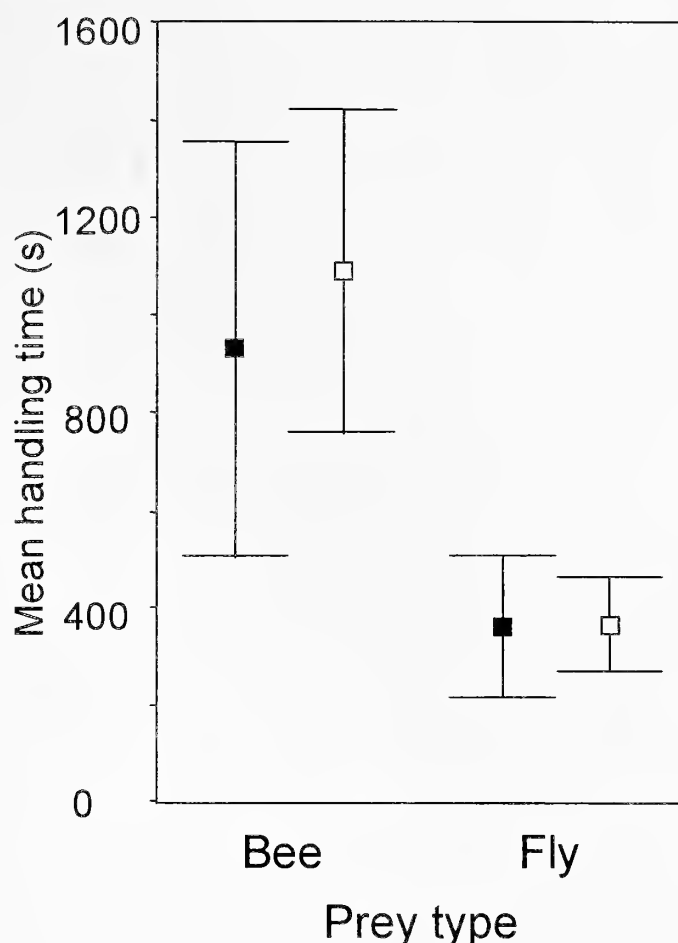


Figure 2.—Effect of prey risk on handling time by small (black box) and large (white box) spiders. Mean \pm 95% Confidence limits. Sample size = 16 colonies. Values for each colony are the average of three measurements per spider size per prey type. Bee = dangerous prey; Fly = safe prey. ANOVA results: prey type: $F = 21.16$, $P = 0.001$; spider size: $F = 0.34$, ns; interaction term: $F = 0.3$, ns. Note that critical P -value (α) = 0.018 through Bonferroni adjustment. $Df = 1, 60$ in all cases.

of hunger is one of the basic factors determining the feeding occurrence and the amount of food an organism ingests. In spiders, the food ingested stays in the gut for a long period of time and a wide range of hunger levels can develop (Nakamura 1987). Therefore, spiders may assess their level of hunger and trade off the need to capture prey against the risks associated with prey capture. Hunger stress increases a spider's willingness to accept the risks and energy expenditure associated with prey capture (Lubin & Henschel 1996).

Based on our experimental analyses we concluded that behavioral tasking in prey capture does not occur in *S. mimosarum*. The only hint of tasking was in the greater number of bites by large spiders (interpreted here as a non-significant difference). There may be therefore a hint that larger spiders are dedicating more effort to prey capture than smaller spiders, whereas smaller spiders may allocate

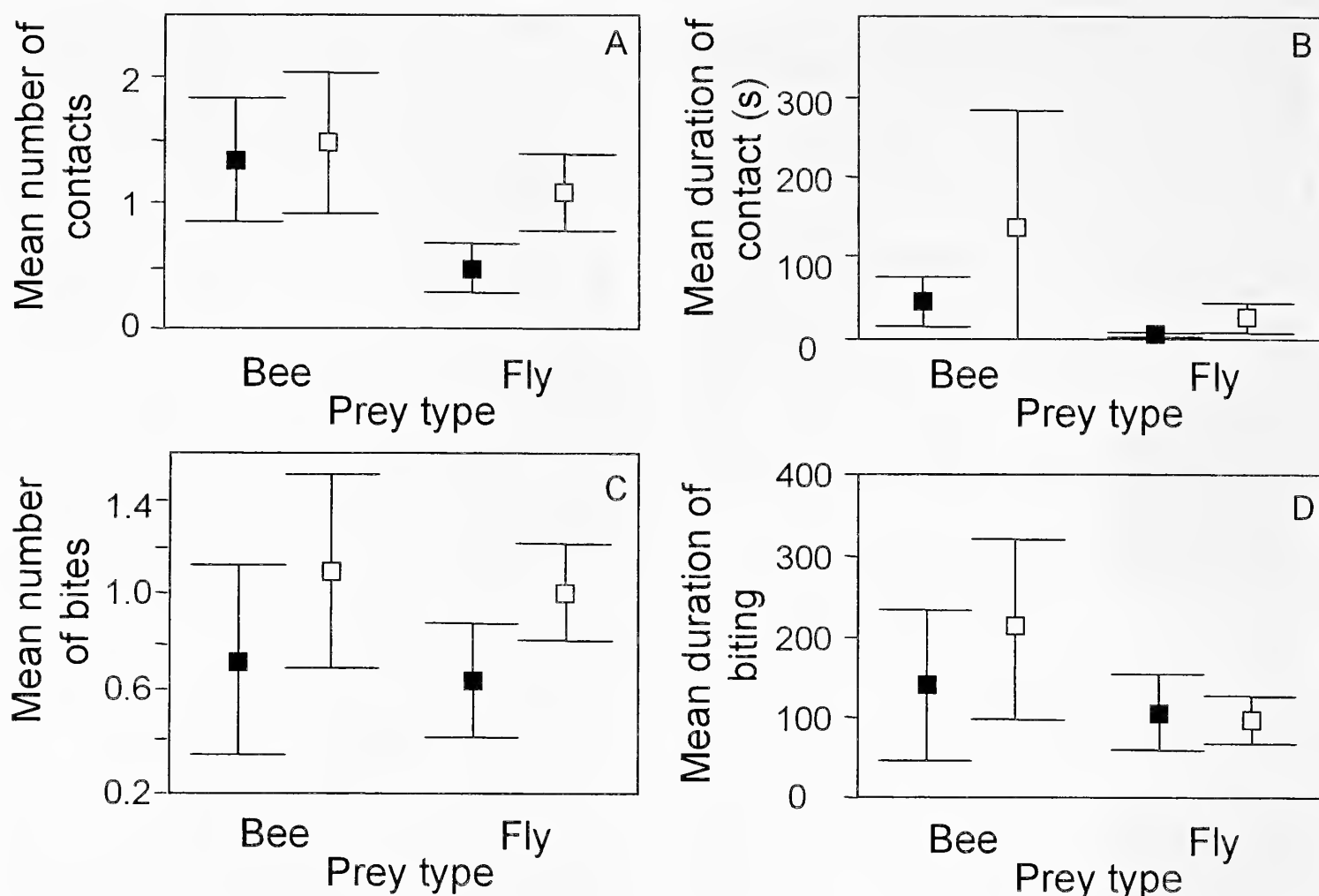


Figure 3.—Effect of prey risk on propensity to attack by small (black box) and large (white box) spiders. Mean \pm 95% confidence limits of: (A) number of contacts. ANOVA results: Prey type: $F = 10.3$, $P = 0.002$; spider size: $F = 3.7$, ns; interaction term: $F = 1.4$, ns. (B) Duration of contacts. ANOVA results: Prey Type: $F = 4.67$, ns ($P = 0.035$); spider size: $F = 2.49$, ns; interaction term: $F = 0.99$, ns. (C) Number of bites. ANOVA results: Prey type: $F = 0.32$, ns; spider size: $F = 5.95$ ns ($P = 0.018$); interaction term: $F = 0$, ns. (D) Duration of bites. ANOVA results: Prey type: $F = 4.07$, ns ($P = 0.048$), spider size: $F = 0.64$, ns; interaction term: $F = 1.2$, ns. Sample size = 16 colonies. Values for each colony are median of three replicates per spider size per prey type. Bee = dangerous prey; Fly = safe prey. Note that critical P -value (α) = 0.018 through Bonferoni adjustment. Df = 1, 60 in all cases.

relatively more effort to other activities. This aspect needs to be further investigated by examining, for example, web building. Overall, we found no statistically significant indication of behavioral tasking, either within foraging or among foraging and other behaviors.

Task differentiation or division of labor has been observed in several species of Hymenoptera and Isoptera (Hermann 1979; Seeley 1985; King's College Socio-biology Group 1982; Lin & Michener 1972), as well as lions (Stander 1992), and mole-rats (Jarvis 1981; Jarvis et al. 1994). No evidence of task differentiation was found for *S. mimosarum*, nor has previous work on these spiders identified any form of division of labor in social *Stegodyphus* (Ward & Enders 1985; Cobby 1981 cited in Seibt & Wickler 1988). The social theridiid spider, *Achaearanea wau* Levi, also showed no division of labor with respect to

foraging and other web-related activities (Lubin 1995). Darchen and Delage-Darche (1986) stated that although the presence of castes in social insects is a fundamental characteristic of eusociality, any attempt to find them in social spiders has been unsuccessful.

There is some support for tasking in *Aneides eximus* Simon, which may have reproductive division of labor (see Rypstra 1993). In *A. eximus* not all individuals reproduce, and under conditions where there is competition for resources, dominance asymmetries result in larger spiders gaining access to more resources, maturing faster, and reproducing (Rypstra 1993). As a consequence of lack of access to resources, small individuals do not breed. However, there is no suggestion that the small spiders forego reproduction in order to undertake some other task that would benefit them or, in the case of *A. eximus*, the

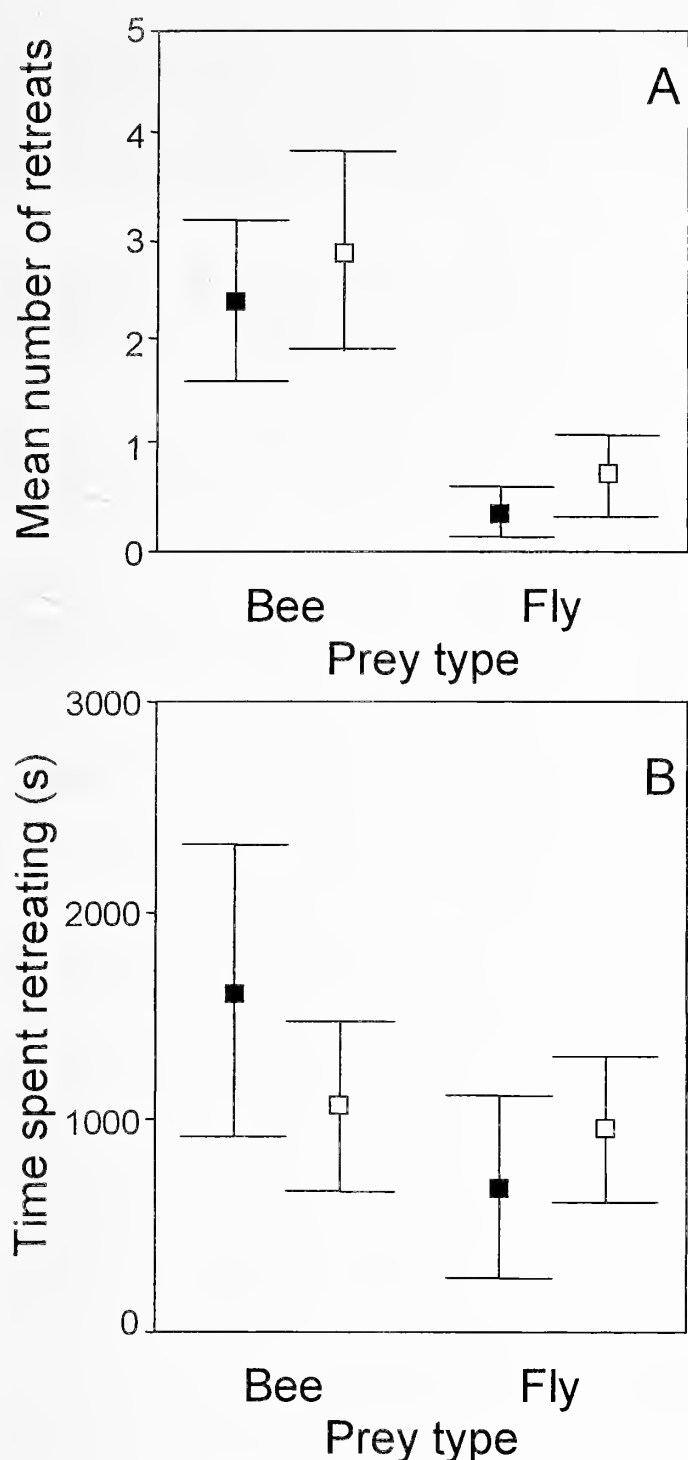


Figure 4.—Effect of prey risk on propensity to retreat by small (black box) and large (white box) spiders. Mean \pm 95% Confidence limits of: (A) number of retreats. ANOVA results: Prey type: $F = 40.79$, $P < 0.001$; spider size: $F = 1.66$, ns; interaction term: $F = 0.04$, ns. (B) Time spent retreating. ANOVA results: Prey size: $F = 4.79$, ns; spider size: $F = 0.3$, ns; interaction term: $F = 2.91$, ns. Sample size = 16 colonies. Values for each colony are the average of three measurements per spider size per prey type. Bee = dangerous prey; Fly = safe prey. Note that critical P -value (α) = 0.018 through Bonferoni adjustment. Df = 1, 60 in all cases.

related colony. We believe that this is not so much an example of selection for behavioral tasking but rather an unselected consequence (effect) of dominance asymmetries (Lubin 1995).

In conclusion, task differentiation with respect to foraging does not appear to exist in these social spider colonies. It should however be noted that, due to the design of the experiment, the behavior of the spiders was observed only until the stage at which the prey was completely subdued. Future work should examine the possibility of role differentiation in other activities such as web construction or brood care.

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CYTOGENETIC HETEROGENEITY IN COMMON HAPLOGYNE SPIDERS FROM ARGENTINA (ARACHNIDA, ARANEAE)

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ABSTRACT. The spermatogenesis of four species of haplogyne spiders from Argentina is analyzed. *Dysdera crocata* (Dysderidae) ($n = 5 + X_0$) has holokinetic chromosomes, achiasmatic male meiosis and a post-reductional division of the sex chromosome. *Ariadna boesenbergii* (Segestriidae) ($n = 4 + X_0$) also possesses holokinetic chromosomes, but meiosis is chiasmatic and the X chromosome divides pre-reductionally. *Kukulcania hibernalis* (Filistatidae) ($n = 11 + X_1X_2X_3$) and *Scytodes globula* (Scytodidae) ($n = 6 + X_0$) have metacentric and submetacentric chromosomes, chiasmatic meiosis and the sex chromosomes divide pre-reductionally. *Kukulcania hibernalis* possesses a bimodal karyotype and a particular chromatin coiling during prophase I, while *Scytodes globula* has striking proximal localization of chiasmata. These results show that Haplogynae present high cytogenetic heterogeneity: species with holokinetic chromosomes as well as species with monocentric chromosomes (metacentric and submetacentric), and species with low diploid numbers, achiasmatic meiosis and proximal chiasma localization.

Keywords: Haplogyne, cytogenetics, meiosis

Phylogenetic knowledge of the higher systematics of Araneae has greatly increased recently (Coddington & Levi 1991; Griswold et al. 1999), and relationships have been analyzed largely on the basis of morphological characters. Cladistic evidence suggests that classical Haplogynae were originally defined on the basis of a plesiomorphy: absence of

fertilization ducts in females, a character considered as primitive. Nevertheless, Filistatidae, Dysderoidea and the remaining “scytodoids” are considered a monophyletic group (Coddington 1990a, 1990b; Coddington & Levi 1991; Platnick et al. 1991; Griswold et al. 1999). This work is aimed to provide cytogenetic data that will be useful for assessing

Table 1.—Karyotype characteristics and collecting locality of the haplogyne species cytogenetically analyzed.

Species	2n	n (male)	Locality	References
Dysderidae				
<i>Dysdera crocata</i> C.L.Koch 1839	11	5+X0	Argentina	This work
<i>D. crocata</i>		?+X0	Uruguay	Benavente & Wettstein 1977,1980; Benavente 1982 (<i>sub D. crocata</i>)
<i>D. magna</i> Keyserling 1877	9	4+X0	Uruguay	Díaz & Sáez, 1966a, 1966b
Filistatidae				
<i>Kukulcania hibernalis</i> (Hentz 1842)	24	11+X ₁ X ₂ 0	Argentina	This work
Pholcidae				
<i>Crossopriza lyoni</i> (Blackwell 1867)	24	11+X ₁ X ₂ 0	India	Sharma et al. 1959
<i>Pholcus crypticolens</i> Bösenberg & Strand 1906	24	11+X ₁ X ₂ 0	Japan	Suzuki 1954
<i>P. phalangoides</i> (Fuesslin 1775)	24	11+X ₁ X ₂ 0	Argentina	Rodríguez Gil et al. 2000
<i>Physocyclus californicus</i> Chamberlin & Gertsch 1929	15	7+X0	U.S.A.	Cokendolpher 1989
<i>P. enaulus</i> Crosby 1926	15	7+X0	U.S.A.	Cokendolpher 1989
<i>Physocyclus</i> sp.	15	7+X0	U.S.A.	Cokendolpher 1989
<i>Spermophora senoculata</i> (Dugès 1836)		?+X ₁ X ₂ 0	U.S.A.	Painter 1914 (<i>sub Spermaphora meridionalis</i> Hentz 1841) (sic!)
Scytodidae				
<i>Scytodes globula</i> Nicolet 1849	13	6+X0	Argentina	This work
<i>S. globula</i>	13	6+X0	Uruguay	Díaz & Sáez 1966a, 1966b (<i>sub S. maculata</i> Holmberg 1876)
Segestriidae				
<i>Ariadna boesenbergii</i> Keyserling 1877	9	4+X0	Argentina	This work
<i>A. mollis</i> (Holmberg 1876)	9	4+X0	Uruguay	Díaz & Sáez 1966a, 1966b
<i>A. lateralis</i> Karsch 1881	7	3+X0	Japan	Suzuki 1954
? <i>Segestria florentina</i> (Rossi 1790)		?+X ₁ X ₂ 0	Uruguay	Benavente & Wettstein 1980; Benavente 1982 (possibly misidentified. Most probably <i>S. ruficeps</i>)
<i>S. ruficeps</i> Guérin 1832	14	6+X ₁ X ₂ 0	Uruguay	Díaz & Sáez 1966a
<i>S. senoculata</i> Linne 1758	14	6+X ₁ X ₂ 0	Japan	Suzuki 1954
Sicariidae				
<i>Loxosceles laeta</i> (Nicolet 1849)	23	10+X ₁ X ₂ Y	Perú	Silva 1988
<i>L. reclusa</i> Gertsch & Mulaik 1940	18	8+X ₁ X ₂ 0	U.S.A.	Tugmon et al. 1990
? <i>L. rufescens</i> (Dufour 1820)	20		Brazil	Beçak & Beçak 1960 (possibly misidentified, see Silva 1988, Tugmon et al. 1990)
? <i>L. rufipes</i> (Lucas 1834)	20	9+X ₁ X ₂ 0	Uruguay	Beçak & Beçak 1960; Díaz & Sáez 1966a (possibly misidentified, see Silva 1988, Tugmon et al. 1990)

relationships among basal members of the Araneomorphae.

Araneae comprises about 108 families and more than 3000 described genera (Platnick 2001). Cytogenetic data in the order, based on about 100 genera and 300 species, reveal the presence of acrocentric and telocentric chromosomes, a male diploid number between 7 and 94, with most species having 2n = 22, 24 or 28, a multiple sex chromosome determining system X₁X₂0/X₁X₁X₂X₂ (85% of the species) and chiasmatic meiosis (Suzuki 1954; White

1973; Maddison 1982, 1996; Gowan 1985; Tugmon et al. 1990; Scioscia 1997). Of these species, only 6% belong to the Haplogynae, and they show particular heterogeneous cytogenetic features that differ from the general characteristics of the order. Cytogenetic data in haplogyne spiders are summarized in Table 1.

Within Haplogynae the genera *Dysdera* Latreille 1804 (Dysderidae), *Segestria* Latreille 1804 and *Ariadna* Savigni & Audouin 1825 (Segestriidae) display holokinetic chromo-

somes (chromosomes with diffuse kinetic activity due to the presence of non-localized centromeres) (Rieger et al. 1991), and achiasmatic meiosis (Appels et al. 1998) has been suggested in *Dysdera* and *Segestria* (Díaz & Sáez 1966a, 1966b; Benavente & Wettstein 1977, 1980; Benavente 1982). The presence of holokinetic chromosomes has been reported in a few invertebrate groups and in some plants, which indicates its polyphyletic origin (White 1973; Grant 1989; Greilhuber 1995; Vanzela et al. 1998). Although entire orders possess this chromosomal type (e.g., Odonata, Heteroptera, Homoptera, Phthiraptera) (Ueshima 1979; Mola 1995; Spence & Blackman 1998; Tombesi et al. 1999), within the Arachnida, holokinetic chromosomes are present in buthid scorpions (Shanahan 1989) and mites of the suborder Prostigmata (Oliver 1977), besides the spider genera already mentioned.

Achiasmatic meiosis has been reported in different invertebrate groups and, among plants, only in the *Fritillaria japonica* group (Liliaceae) (John 1990). This type of meiosis has originated independently, and appears to be a secondarily acquired feature from a chiasmatic meiosis, since in Diptera, mantids and enchytroids achiasmatic meiosis is found in the more advanced forms (John 1990; Appels et al. 1998). In Arachnida, achiasmatic meiosis has been also described in scorpions of the family Buthidae (Shanahan 1989).

In the present work, four species belonging to the spider group Haplogynae have been cytogenetically analyzed: *Ariadna boesenbergii* Keyserling 1877 (Segestriidae), *Dysdera crocata* C. L. Koch 1839 (Dysderidae), *Kukulcania hibernalis* (Hentz 1842) (Filistatidae) and *Scytodes globula* Nicolet 1849 (Scytodidae).

METHODS

The following specimens from Argentina were analyzed (number of individuals and collecting locality are indicated):

Dysdera crocata: 9 individuals (4 males, 2 immatures and 3 females). Ciudad Autónoma de Buenos Aires and Río Luján (Buenos Aires Province).

Ariadna boesenbergii: 27 individuals (7 males, 2 subadult males, 10 immatures and 8 females). Ciudad Autónoma de Buenos Aires.

Kukulcania hibernalis: 27 individuals (22 males, 1 subadult male, 3 immatures and 1 subadult female). Ciudad Autónoma de Buenos Aires, Rojas, Martín García Island Natural Preserve and Buenos Aires city surroundings (Buenos Aires Province); and Departamento Capital (Tucumán Province). *Scytodes globula*: 13 individuals (5 males, 6 subadult males, and 2 immatures). Martín García Island Natural Preserve, Río Luján and Buenos Aires city surroundings (Buenos Aires Province).

Voucher specimens are deposited in the Museo Argentino de Ciencias Naturales (MACN) Arachnology collection.

The specimens of *A. boesenbergii* were mainly collected from *Tipuana tipu* trees, while the remaining specimens were collected from houses and neighboring constructions. Living specimens were bred at the Arachnology Department of the MACN.

Individuals were fixed in 3:1 (absolute ethanol:glacial acetic acid); gonads were dissected out and slides were performed by the squash method in iron propionic haematoxylin (Núñez 1968).

RESULTS

Mitotic and meiotic cells suitable for cytogenetic analysis were only observed in 4 males of *Dysdera crocata*; 1 male, 2 subadult males and 2 immatures of *Ariadna boesenbergii*; 6 males and 1 subadult male of *Kukulcania hibernalis*; and 4 males, 4 subadult males and 1 immature of *Scytodes globula*.

Dysdera crocata: this species is $2n = 11$, $n = 5 + X0$ (male). In spermatogonial mitoses three larger chromosomes are detected (one autosomal pair and the X chromosome), and the lack of a primary constriction is evident (holokinetic chromosomes) (Figs. 1A, B). At meiotic prophase I the sex chromosome is positively heteropycnotic. After pachytene no typical diplotene or diakinesis stages are observed, due to the absence of chiasmata. Bivalents decondense later originating a homogeneous chromatin mass with the X still positively heteropycnotic (Fig. 1C). The chromatin mass then divides into 2 or 3 blocks (Figs. 1D, E). Bivalents continue separating except for the two smaller which remain associated (Fig. 1F). At prometaphase I the X chromosome turns isopycnotic, and among

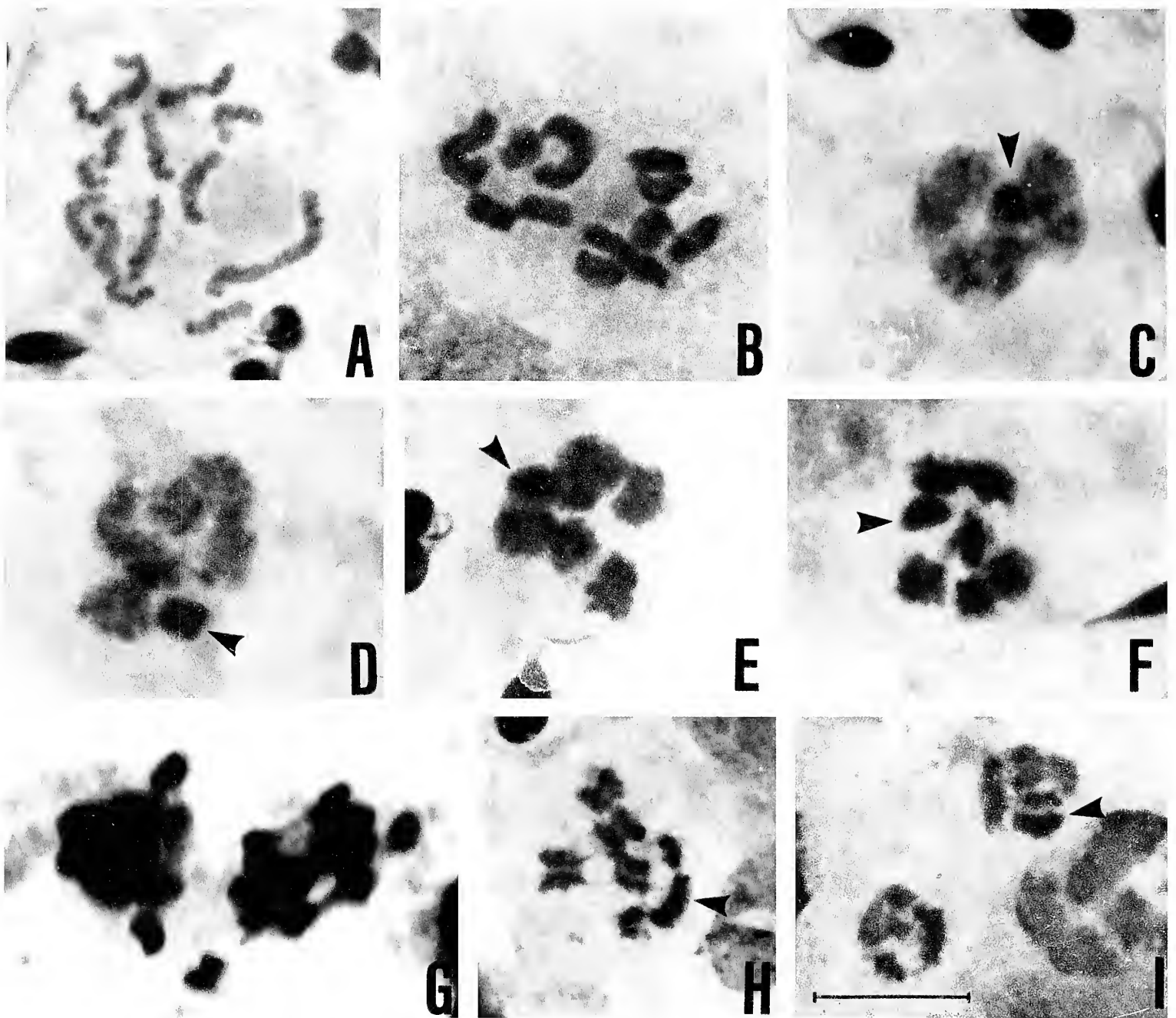


Figure 1.—*Dysdera crocata* ($2n = 11$, $n = 5 + X0$) A) Mitotic prophase. B) Mitotic prometaphase. C-E) Prophase I. F) Prometaphase I. G) Anaphase I. H) Metaphase II; one chromosome has already separated its chromatids. I) Telophase II. Scale = 10 μm . Arrowheads point to the X chromosome.

autosomal bivalents one larger and four of similar size are recognized. At anaphase I the sex chromosome divides precociously and equationally, separating sister chromatids (Fig. 1G). At metaphase II the autosomes lie with their long axis parallel to the equatorial plane while the X lies at the periphery (Fig. 1H). The sex chromosome divides reductionally at anaphase II, originating telophase II nuclei with and without the sex chromosome (Fig. 1I).

Ariadna boesenbergii: this species is $2n = 9$, $n = 4 + X0$ (male). At spermatogonial prophase it is evident that chromosomes are holokinetic, and five larger chromosomes are distinguished (two autosomal pairs and the X chromosome) (Figs. 2A, B). At meiotic prophase the sex chromosome is slightly posi-

tively heteropycnotic. At diplotene two large and two small bivalents are observed, while the X chromosome is even a little smaller than the latter. At diakinesis the largest bivalents always possess two chiasmata while the smaller ones generally have only one chiasma. Mean chiasma frequency is 7.02 (Fig. 2C), and occasionally three chiasmata are formed in large bivalents. At metaphase I the sex chromosome is out of plate (Fig. 2D) and at anaphase I it migrates undivided to one pole, lagging behind the autosomes (pre-reductional division) (Fig. 2E). At metaphase II the chromosomes lie with their long axis parallel to the equatorial plane (Figs. 2F, G). The X chromosome divides equationally and precociously at anaphase II (Fig. 2H).

Kukulcania hibernalis: this species is $2n =$

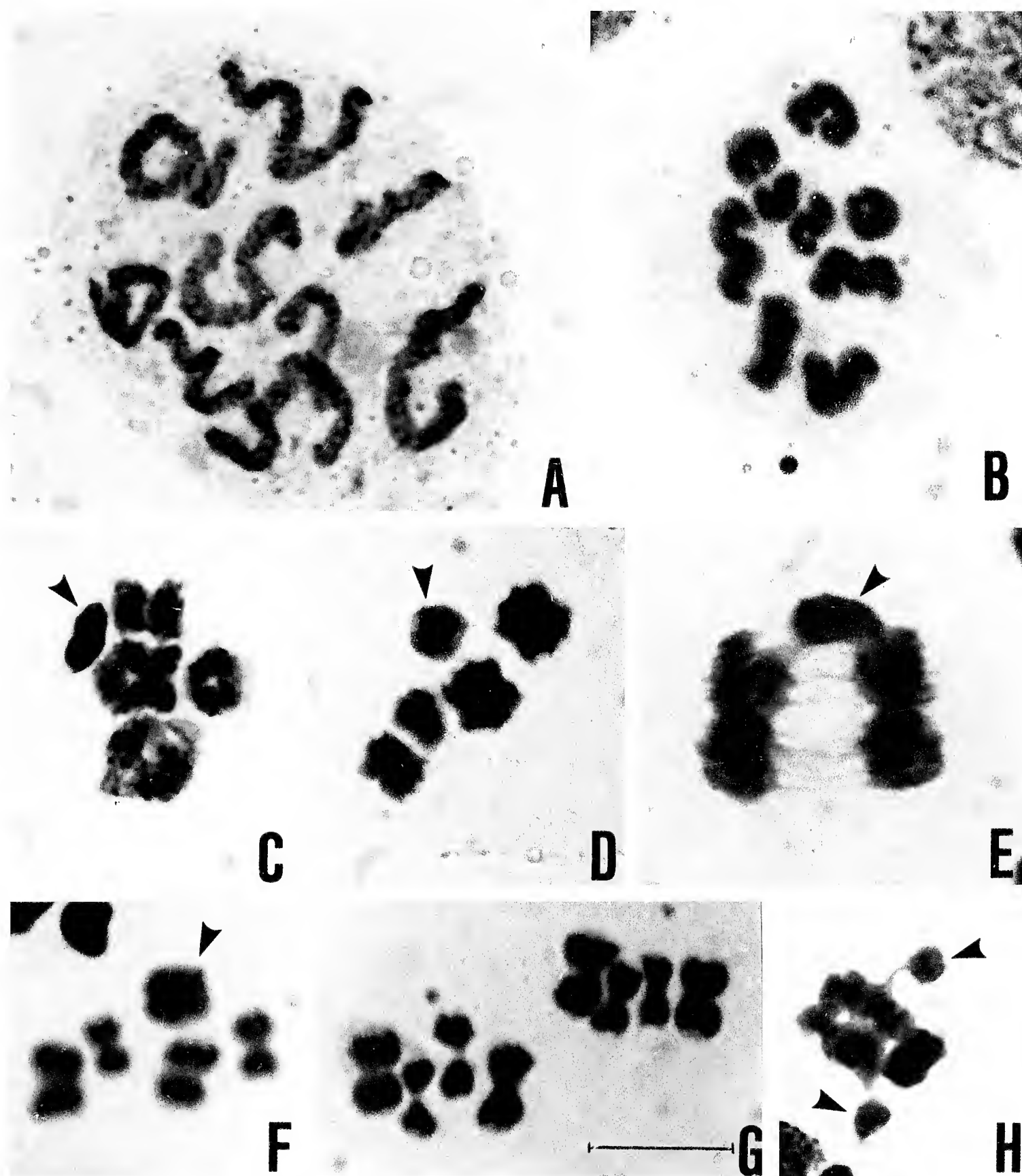


Figure 2.—*Ariadna boesenbergii* ($2n = 9$, $n = 4 + X0$). A) Mitotic prophase. B) Mitotic prometaphase. C) Diakinesis with three ring bivalents. D) Metaphase I. E) Anaphase I. F) Metaphase II with X chromosome. G) Metaphases II without X chromosome. H) Anaphase II. Scale = 10 μm . Arrowheads point to the X chromosome.

24, $n = 11 + X_1X_20$ (male), with metacentric and submetacentric chromosomes. At spermatogonial prometaphases four extremely large autosomes are distinguished, while the sex chromosomes cannot be identified. At pachytene, bivalents arrange in a bouquet, and no positively heteropycnotic body is observed (Fig. 3A). Bivalents then decondense com-

pletely and enter a diffuse stage in which it is difficult to individualize them. During this long diffuse stage the sex chromosomes are condensed, being positively heteropycnotic and intimately associated (Fig. 3B). One of the large autosomal bivalents does not decondense completely, remaining slightly positively heteropycnotic and usually showing a ring

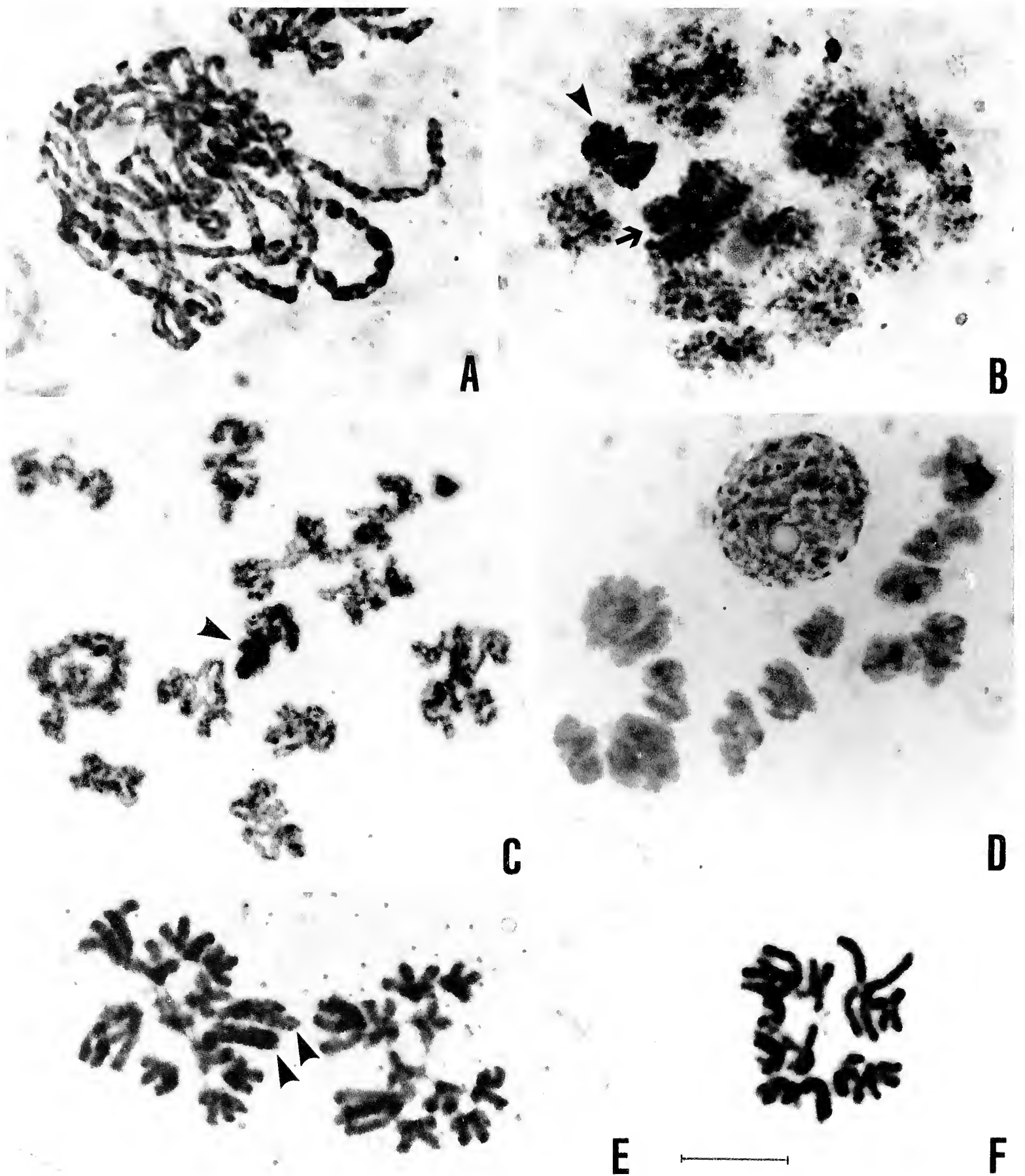


Figure 3.—*Kukulcania hibernalis* ($2n = 24$, $n = 11 + X_1X_20$) A) Pachytene. B) Diffuse stage; arrow points to the less decondensed bivalent. C) Diplotene. D) Prometaphase I. E) Telophase I. F) Metaphase II without X chromosomes. Scale = 10 μm . Arrowheads point to the X chromosome.

shape. The other large bivalent is frequently observed associated to a nucleolus. At diakinesis bivalents recondense adopting a particular morphology, and the sex chromosomes continue positively heteropycnotic (Fig. 3C). Bivalents present one chiasma except one of the larger ones that generally presents two chi-

asmata. At prometaphase I bivalents and the sex chromosomes are isopycnotic (Fig. 3D). At anaphase I the sex chromosomes (X_1X_2) migrate together to the same pole (pre-reductional division) (Fig. 3E); it is clear that the sex chromosomes are large and unequal in size. This species presents two kinds of meta-

phase II, with and without sex chromosomes (11 autosomes + X_1X_2 and 11 autosomes, Fig. 3F). At the second meiotic division the sex chromosomes divide equationally.

Scytodes globula: this species is $2n = 13$, $n = 6 + X0$ (male), with metacentric and submetacentric autosomes of similar size, and a submetacentric sex chromosome. At early prophase I the X chromosome is positively heteropycnotic (Fig. 4A). At diplotene and diakinesis it is evident that all bivalents present one chiasma next to the centromere (Fig. 4B, C). A few cells with one bivalent with two chiasmata have been observed; when they have two chiasmata, one is proximal and the other distal (Fig. 4B). At metaphase I the sex chromosome lies outside the equatorial plate (Fig. 4D), and at anaphase I it migrates undivided to one pole lagging behind the autosomes (pre-reductional division) (Fig. 4E). Metaphases II with (Fig. 4F) and without the sex chromosome are observed. At anaphase II the X chromosome divides equationally and synchronously with the autosomes. Telophase II nuclei with and without sex chromosomes are observed (Fig. 4G). At both anaphase I and anaphase II the sex chromosome is thinner and larger than the autosomes, and it is slightly negatively heteropycnotic.

DISCUSSION

Cytogenetic studies on haplogyne spiders reveal marked differences from the general characteristics of the order: the presence of holokinetic chromosomes and achiasmatic meiosis have been reported in some species of Dysderidae and Segestriidae; and in species with monocentric chromosomes, the metacentric and submetacentric morphology is frequent. The diploid chromosome numbers of these species are the lowest or among the lowest known for the order ($2n = 7$ to $2n = 24$).

Previous reports on *Dysdera* agree with our results utilizing Argentinean individuals of *Dysdera crocata* with reference to the holokinetic nature of its chromosomes, the post-reductional division of the sex chromosome, the achiasmatic meiosis and the low chromosome number (Table 1) (Díaz & Sáez 1966a, 1966b; Benavente & Wettstein 1977, 1980; Benavente 1982). However, karyotypic data on *D. crocata* were absent (Benavente & Wettstein 1977, 1980; Benavente 1982).

Within the Segestriidae, the genera *Ariadna*

and *Segestria* have been studied (Table 1). Díaz & Sáez (1966b) described in *Ariadna mollis* (Holmberg 1876) a haploid number of $n = 4 + X0$ with holokinetic chromosomes, and Suzuki (1954) described $n = 3 + X0$ in *A. lateralis* Karsch 1881. *Ariadna boesenbergii* ($n = 4 + X0$) presents the same sex chromosome determining system and also a low diploid number. In this species, as well as in *A. lateralis* (Suzuki 1954) the sex chromosome migrates late and pre-reductionally, and these observations bring us to suggest that the "lagging bivalent" described by Díaz & Sáez (1966b) in *A. mollis* at anaphase I is a misinterpretation of the lagging X chromosome. *Segestria ruficeps* and *S. senoculata* also present a low chromosome number, but a multiple sex chromosome determining system ($X_1X_20/X_1X_1X_2X_2$) (Table 1). In *S. florentina* (most probably *S. ruficeps*) Benavente & Wettstein (1980) described the presence of holokinetic chromosomes, achiasmatic meiosis and pre-reduction of the sex chromosomes.

In summary, Segestriidae and Dysderidae share two cytogenetic traits uncommon within the order, and even in the animal kingdom: holokinetic chromosomes and achiasmatic male meiosis. The fact that the only three genera cytogenetically analyzed until now have holokinetic chromosomes should suggest that this characteristic could have had a common origin; on the other hand, the absence of chiasmata in *Dysdera* and *Segestria* could have originated independently, since it is not a common feature to both families.

Kukulcania hibernalis and *Scytodes globula* are the only species of Filistatidae and Scytodidae cytogenetically analyzed. The chromosome number of *Kukulcania hibernalis* is one of the most frequent in the order, and its sex determining mechanism is typical of Araneae, although it differs since it has metacentric and submetacentric chromosomes, and a bimodal karyotype. On the other hand, *Scytodes globula* also displays characteristics uncommon to the order: a low diploid number, metacentric and submetacentric chromosomes, and a proximal chiasma localization, which causes the particular bivalent morphology. Díaz & Sáez (1966a, 1966b) studied males of *Scytodes globula* from Uruguay, and they found the same chromosome number and similar meiotic characteristics to those described here.

It is noteworthy that in the species here an-

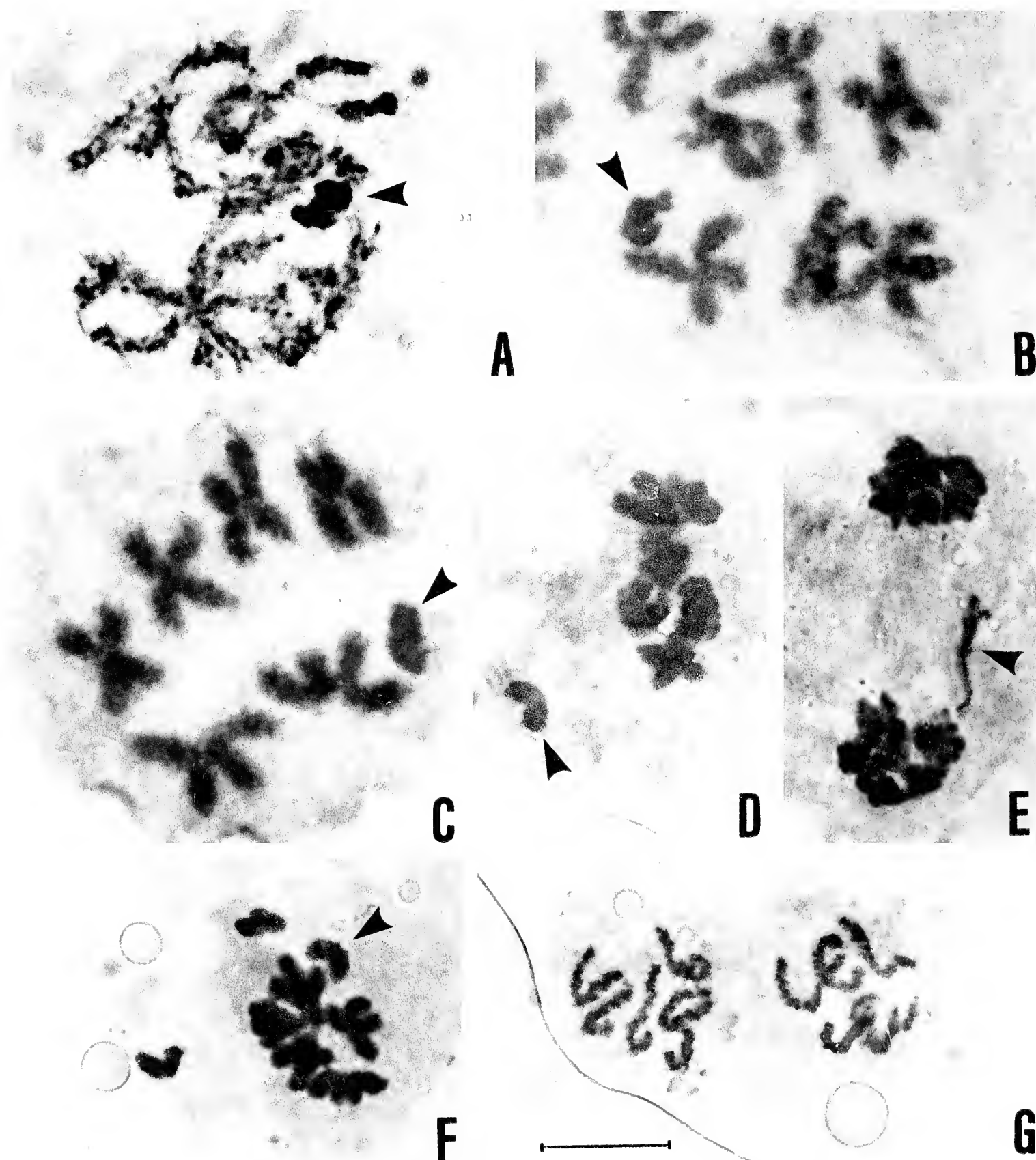


Figure 4.—*Scytodes globula* ($2n = 13$, $n = 6 + X0$). A) Early diplotene. B-C) Diakinesis. D) Metaphase I. E) Telophase I. F) Metaphase II; one chromosome has already separated its chromatids. G) Telophase II without X chromosome. Scale = 10 μm . Arrowheads point to the X chromosome.

alyzed there are marked differences in the cycle and degree of chromatin condensation during meiosis I, although during meiosis II the chromosome morphology is in accordance with that usually observed in spiders. More studies on chromatin organization and coiling are necessary in order to explain this uncommon behaviour.

The number and position of chiasmata, and even its absence, are under genetic control

(Appels et al. 1998). Most organisms present a random chiasma distribution, and the number of chiasmata is related to the chromosome length, among other characteristics. In some species, an extreme chiasma localization in distal regions, and less frequently in proximal ones, has been described (John 1990). In insects, proximal chiasma localization has been described in Orthoptera with telocentric chromosomes (John 1990), and *S. globula* is an

example of proximal chiasma localization in metacentric chromosomes. Chiasma localization has genetic consequences since it leads to the appearance of large linkage groups, which are inherited as a unit, constraining the occurrence of recombination and hence, the generation of genetic variability.

Cytogenetic data in Dysderidae, Segestriidae, Filistatidae and Scytodidae are heterogeneous in many respects: kinetic activity (monocentric or holokinetic chromosomes); chromosome number, size and morphology; sex chromosome determining system; type of division of the sex chromosomes (pre- or post-reductional), and chiasma frequency and distribution. This cytogenetic heterogeneity raises many questions about the meiotic system and karyotype evolution within Haplogynae, and a more exhaustive study in other species of basal araneomorph spiders and even mygalomorph groups is necessary in order to explain the diversity encountered. This work is a first approach to the cytogenetic characterization of this spiders group. Further cytogenetic data together with morphological ones will contribute to a better understanding of the phylogenetic relationships in haplogyne spiders.

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VALIDATION OF A SIMPLE METHOD FOR MONITORING AERIAL ACTIVITY OF SPIDERS

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ABSTRACT. Many species of spider disperse by ballooning (aerial dispersal), and indices of aerial activity are required in studies of population dynamics and biological control in field crops where spider immigrants are needed for pest suppression. Current methods (e.g., suction traps, sticky traps, deposition traps) of monitoring aerial activity are very labor-intensive, expensive, or require a power supply. We tested Ballooning Index (BI), an alternative, simple method utilizing inexpensive equipment. This method involved the monitoring of spiders climbing an array of 30 cm tall wooden sticks placed vertically in short turf. During a two-year study in arable land in the UK, the incidence of spiders (mainly Linyphiidae) on sticks was correlated with the numbers caught at 1.4 m and 12.2 m above ground in suction traps. Climbing activity on sticks was greater during the morning than in the afternoon, and this activity started progressively earlier in summer than in winter. There was no seasonal change in the proportion of spiders caught at the two heights in suction traps. The pattern of catches (on sticks and in suction traps) suggested strongly that the majority of ballooning spiders dispersed by a number of short flights, rather than by a single long flight, and that segregation of immigrants and emigrants is not possible by any current method. The BI method appears to be, however, a simple and reliable technique for monitoring the overall aerial activity of ballooning spiders.

Keywords: Aerial dispersal, ballooning height, seasonal variation, Linyphiidae, Araneae

Spiders are generalist predators that may be of great importance in reducing, and even preventing, outbreaks of insect pests in agriculture (Riechert & Lockley 1984; Sunderland et al. 1986). Hence it might be profitable to create and sustain high densities of spiders in fields. However, agricultural cultivations kill spiders and destroy their habitats (Thomas & Jepson 1997; Topping & Sunderland 1998). Furthermore, fields vary in their suitability as habitats for spiders over the growing season of the crop (Dinter 1996). Therefore the ability to disperse well is vital for the persistence and survival of spiders in agricultural habitats (Weyman 1993 and references therein). Re-colonization of the fields is normally by aerial dispersal rather than by cursorial movements (Bishop & Riechert 1990), but this varies

among species (Thomas et al. 1990). Several studies have suggested that spider dispersal and re-colonization of fields are significant aspects of spider population dynamics in agroecosystems (Bishop & Riechert 1990; Nyffeler & Breene 1990; Dinter 1996; Thomas & Jepson 1997; Topping & Sunderland 1998; Thomas et al. 1990). Therefore, to understand the population and spatial dynamics of spiders in arable land, it is necessary to study their dispersal.

Aerial dispersal of spiders has proven laborious and expensive to measure (Topping & Sunderland 1995). Various methods have been used to monitor aerial activity by spiders, e.g., by suction traps at 12.2 m (Toft 1995; Blandenier & Fürst 1998) and 1.4 m (Topping & Sunderland 1995) above ground, rotary trap (Topping et al. 1992; Topping & Sunderland 1995), deposition traps (Topping & Sunder-

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land 1995; Weyman et al. 1995), sticky traps (e.g., Greenstone et al. 1985; Plagens 1986), and aircraft-mounted trapping devices (Greenstone 1991). They all give good measures of aerial activity, but are not always practical, especially when finances and time are limited. Suction traps require a power supply and are expensive, aircraft-mounted equipment is expensive to use and sticky trap and deposition trap samples (water trays) take a long time to process (Topping & Sunderland 1995).

Here a simple method, utilizing inexpensive equipment, for measuring aerial dispersal of spiders is proposed, i.e., monitoring the number of spiders that climb up wooden sticks placed vertically in closely-mown grass turf (hereafter termed the "Ballooning Index" or BI method). BI is a simple method, which does not require a power supply or much time to process. This is not an entirely new approach; similar methods were used in pioneering studies on spider dispersal (Duffey 1956; van Wingerden & Vugts 1974; Vugts & van Wingerden 1976). Furthermore, Weyman (1995) has shown, under laboratory conditions, that climbing a vertical structure is a part of pre-ballooning behavior, but to our knowledge no one has determined whether attempts at ballooning by spiders on the ground correspond to the aerial density of ballooning spiders. Here we describe our test of whether pre-ballooning behavior on the ground (BI) corresponded well with aerial density as measured by suction traps (at 1.4 m and 12.2 m).

There is likely to be a positive correlation between height of ballooning and distance travelled per flight (Thomas 1992). The latter is of great significance in relation to annual re-colonization of fields from reservoir habitats (Sunderland & Samu 2000). Danish data (Toft 1995) suggest that the majority of spiders balloon closer to the ground during the colder seasons than in summer. If this is true, there will be fewer long-distance migrants (as assessed by the 12.2 m trap) during winter. Hence, BI (being close to the ground) would tend to overestimate the aerial dispersal of spiders, as the spiders would climb the sticks to take off, but would not go very far. Therefore, we tested whether there was a difference in the height at which spiders ballooned at different times of year, to determine whether the findings for Denmark (Toft 1995) also apply in the UK.

METHODS

Study area.—The study was carried out in West Sussex, UK (at grid reference 04TQ 045 035) at the edge (just outside the crop) of a 3 ha winter wheat (cv. Riband) field. The field received normal agrochemical applications but no insecticides were required during the experiment. Adjacent to the field there was a conurbation to the south, east and west and arable land to the north.

Dispersal.—Three methods were used to measure the dispersal activity of spiders: a suction trap at 1.4 m above ground, a suction trap at 12.2 m above ground and BI.

Suction traps: The 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap (Taylor 1955)) sampled air at a rate of 70–75 m³ min⁻¹. The 12.2 m suction trap (Rothamsted Insect Survey Trap) sampled air at a rate of 45–50 m³ min⁻¹ (Macaulay et al. 1988). To standardize the catch from the two suction traps, the catch from the 1.4 m suction trap was multiplied by 0.67 to standardize to 50 m³ min⁻¹.

The 1.4 m and the 12.2 m suction traps were placed 5 m apart on grass just outside the field's southern edge. The suction traps were operated for two years, from April 1990 to December 1991. In 1990 the trap samples were segregated into night and day samples. In 1991 both suction traps sampled 24 h/day and were emptied daily between 0730–1030 h. Each suction sample took on average 10–20 min to process.

BI: The incidence of spiders preparing to balloon was assessed by observing spiders climbing wooden sticks. Twenty cylindrical sticks (40 cm long, 0.5 cm diameter) were set vertically into a lawn (with 30 cm being above ground) in a 5 X 4 grid, each row and column being 60 cm apart. The lawn, which was mown approximately weekly, was sited on the western edge of the winter wheat field at 60 m from the suction traps.

It was assumed that spiders climbed the sticks as part of pre-ballooning behavior. However, as this might not be the case, it was also noted when spiders actually attempted to take off, i.e., showed "tip-toe" behavior. Tip-toe behavior (a stereotyped posture, whereby spiders raise their bodies above the substrate to bring themselves into more rapidly moving air (Richter 1970; Suter 1991)) is a well-

known component of pre-ballooning behavior. The time of day, wind speed and number of spiders climbing the sticks, and whether they showed tip-toe behavior were noted for each observation. The wind speed was measured 1 m above ground by an anemometer attached to a Squirrel® datalogger (Grant Instruments, Cambridge, UK). After each observation (which took approximately 5 min for the 20-stick array), spiders on the sticks were gently brushed off the sticks and onto the grass below. The BI method therefore does not preclude the possibility that some individual spiders are recorded in more than one observation period.

BI was carried out from 24 April–28 November 1991. BI was done only during the daylight hours, as previous studies in the USA have shown that spiders do not initiate ballooning at night (Yeargan 1975; Bishop 1990), and our segregation of day and night suction trap catches confirmed that few spiders balloon at night in UK. Thus, we report observations made between 0700–2200 h. The average number of spiders climbing the sticks per observation was calculated for each day. Comparison between the numbers in suction trap samples and the numbers on BI, were performed for the 78 days when both suction traps were in operation, and BI were observed four or more times.

RESULTS

During the study period we collected a total of 8772 spiders in the 1.4 m high suction trap (uncorrected numbers) and 3781 spiders in the 12.2 m suction trap and we observed 1079 spiders in BI during a total of 649 observations. Linyphiidae constituted 96% and 92% of spiders caught in the 1.4 m and 12.2 m suction traps, respectively. The spiders from BI were not identified to species, but a very high proportion were Linyphiidae.

In order to indicate whether the total number of spiders climbing sticks could be used as a measure of ballooning intent, the number of spiders showing tip-toe behavior was compared with the total number climbing. There was a highly significant correlation ($r = 0.98$, $df = 76$, $P < 0.001$), hence, the total number of spiders climbing was used as response variable. On no occasion were any spiders recorded climbing when wind speed was above 3.5 ms^{-1} .

To see how well BI detected aerial dispersal, the days on which all three methods agreed in detecting occurrence or non-occurrence of dispersal were counted. On 74% of days all three methods agreed, and when only the 1.4 m suction trap and BI were compared there was agreement on 82% of days. The three methods showed a very similar pattern of aerial dispersal, as can be seen in Fig. 1. Most peaks of aerial dispersal (17 of 21) matched in all three methods, but suction traps detected more peaks than did BI, which could be expected as suction traps operate continuously 24 h/day. Not only the pattern but also the magnitude of aerial activity agreed for all three methods. BI showed better correlation with the 1.4 m suction trap ($r = 0.69$, $df = 76$, $P < 0.001$) than with the 12.2 m suction trap ($r = 0.46$, $df = 76$, $P < 0.001$). This was probably due to BI and the 1.4 m suction trap operating at approximately the same height.

Climbing activity was greatest in the morning, and most ballooning attempts had ended before 1300 h (Fig. 2). In summer, activity appeared to peak earlier than in spring and autumn, probably because the sun rises earlier in summer. In July and August climbing activity was already high when BI was started, hence, activity peaks may have been missed. However, the three methods did not differ more in July and August than the rest of the study period (Fig. 1).

The suction traps were better correlated with each other ($r = 0.90$, $df = 76$, $P < 0.001$) than with BI. In general the 1.4 m suction trap caught more spiders than the 12.2 m suction trap. On 84 out of 575 days of sampling the 1.4 m suction trap caught spiders when the 12.2 m trap did not, whereas the opposite was true only on 33 days (Fig. 3). This suggests that more spiders balloon near to the ground, hence the 1.4 m suction trap is a better measure of aerial activity than the 12.2 m trap.

There was no systematic difference in the proportion of spiders caught in 12.2 m and 1.4 m suction traps at different times of year (Fig. 4). Hence there is no indication of spiders failing to reach higher elevations during autumn and winter, at least not at this study site during the two years of sampling.

DISCUSSION

Spiders only climbed the sticks when wind speeds were below 3.5 ms^{-1} which lends

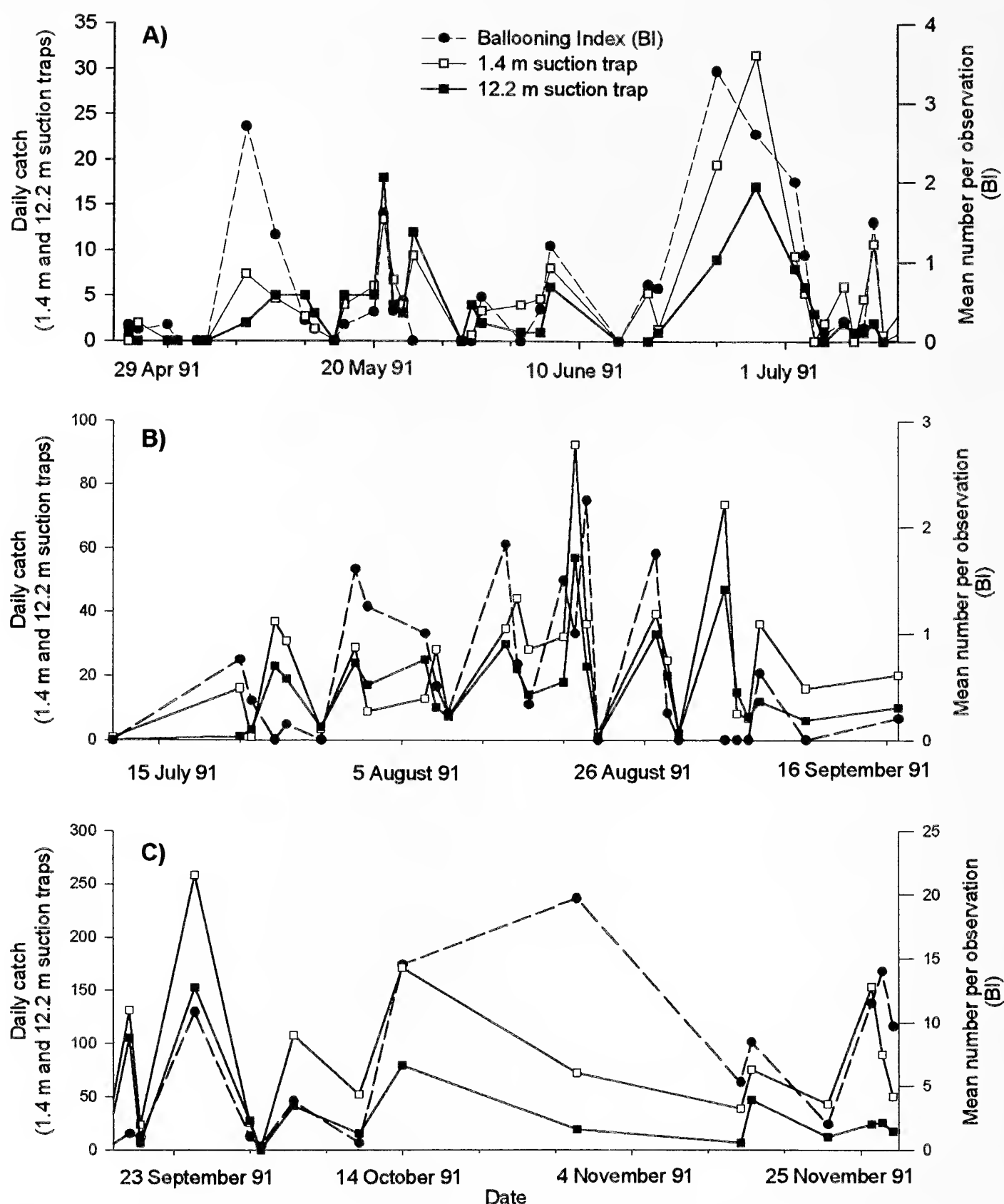


Figure 1.—Ballooning activity measured by BI (monitoring climbing activity of spiders on an array of sticks), 12.2 m suction trap (Rothamsted Insect Survey Trap) and 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap). A) spring and early summer (24 April–11 July 1991). B) late summer (11 July–17 September 1991). C) autumn (17 September–28 November 1991).

weight to the contention that BI is a measure of ballooning activity, because otherwise spiders would also have been expected to climb sticks in weather not suitable for ballooning (Weyman 1993).

The match in the results among the three methods was generally good, thus the pre-ballooning activity of spiders on the ground corresponded well with aerial density. Suc-

tion traps were slightly more sensitive than BI to ballooning activity, which was expected since the suction traps sampled continuously for 24 h/day, and data from BI were from as little as four observations per day. Where there are discrepancies, many of them can probably be explained by the fact that the suction traps were emptied several hours after sunrise, therefore one day's sam-

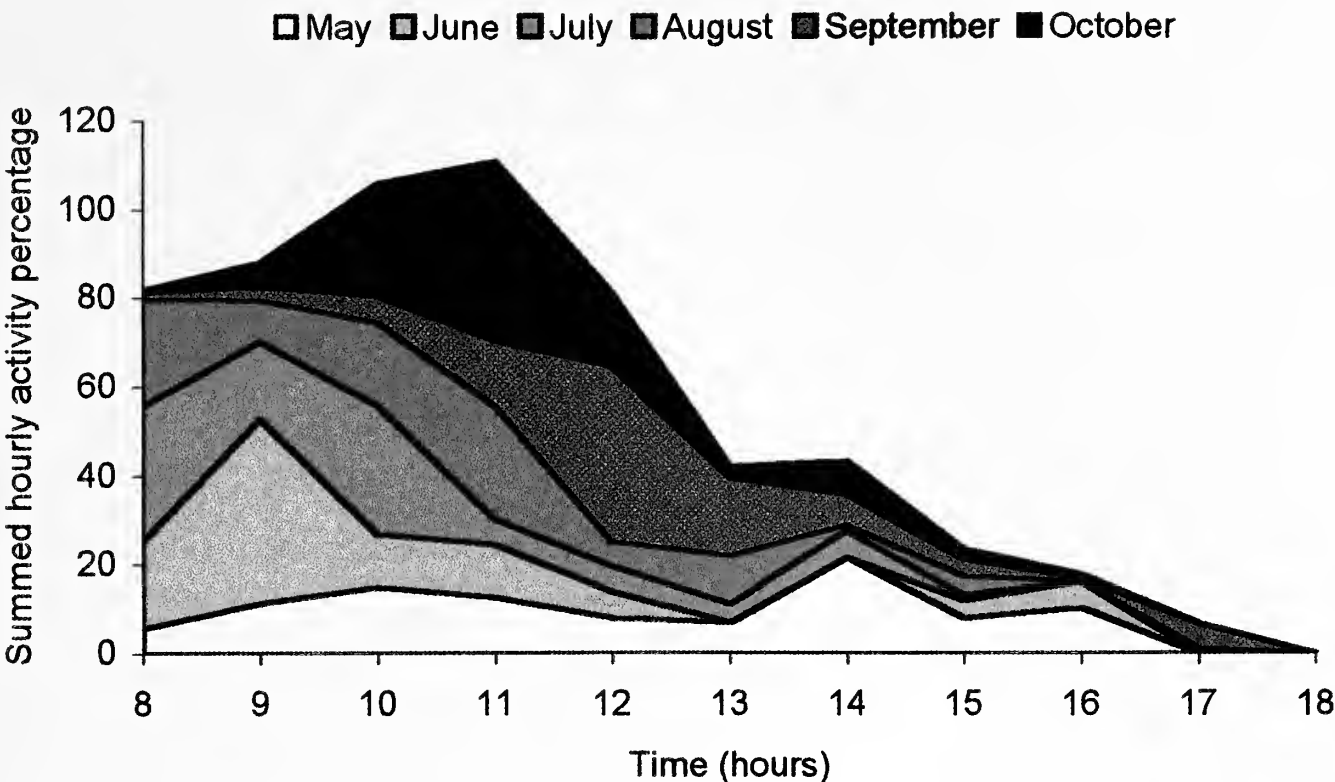


Figure 2.—Observations of spiders climbing sticks (BI) in relation to month and time of day. The hourly activity was calculated separately for each month, and is displayed cumulatively. The hourly activity was calculated as the percentage of spiders climbing at a given hour out of the total numbers of spiders that were observed climbing the sticks that month.

ple could often contain spiders from parts of two days.

Vugts and Van Wingerden (1976) found that ballooning starts 1–4 h after sunrise. This agrees well with our finding that ballooning

started earlier in summer than in spring and autumn. Therefore if BI is used, effort should be concentrated in the morning rather than in the afternoon. To have continuous monitoring of ballooning motivation one could use adhesive-coated sticks as Duffey (1956) did. However, adhesive-coated sticks present other problems. Flying insects clog them during the summer months (Duffey 1956), it takes time to sort the spiders from trapped insects, and at low temperatures the glue becomes too stiff to trap the spiders. Studies may also have to

- Spiders in 12.2 m trap, no spiders in 1.4 m trap
- No spiders in 12.2 m trap, spiders in 1.4 m trap
- Spiders in 12.2 m trap and 1.4 m trap
- No spiders in either 12.2 m trap or 1.4 m trap

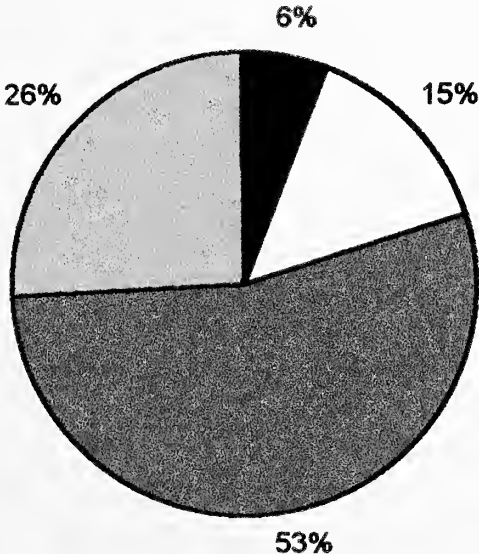


Figure 3.—Detection of aerial activity by 12.2 m suction trap (Rothamsted Insect Survey Trap) and 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap). In total the traps were in operation for 575 days.

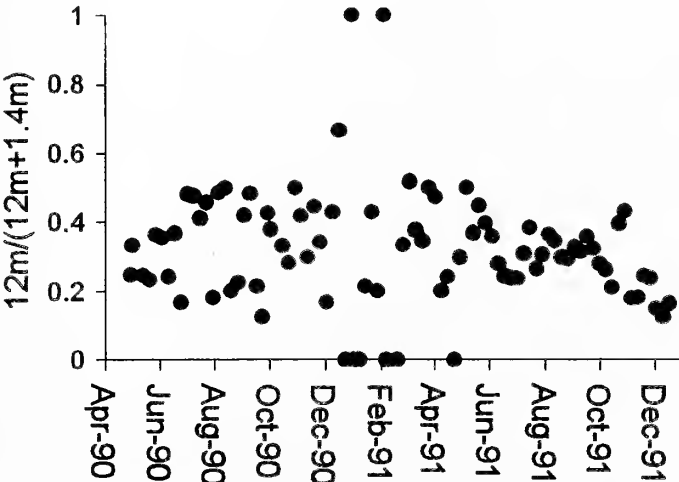


Figure 4.—Relationship between aerial density of spiders at 1.4 m and 12.2 m. The Y-axis is the weekly catch from the 12.2 m suction trap divided by the total weekly catch in both 12.2 and 1.4 m suction traps.

be done to determine how well spiders are trapped by the adhesive, as there seems to be some difference between the sexes (Thomas 1992).

BI may not be appropriate for climbing species that also forage on vegetation, but for Linyphiidae it appears to be a reliable method. We suspect that the method is mainly measuring re-ballooning attempts by grounded aeronauts that landed on the short grass turf and climbed up the nearest vertical structure, as it was not likely that such a small strip of short grass would support a spider population of the size indicated by the number of spiders climbing the sticks. If this is the case, then BI could be used as an index of aerial activity even for the airspace above tall crops, providing that the array of sticks is placed in a cleared area of bare ground or short vegetation (within or at the edge of the tall crop).

In general there was good agreement between different methods for monitoring ballooning activity of spiders. In a previous study (Topping & Sunderland 1995) results from a deposition trap, a 1.4 m suction trap, a rotor trap and sticky traps were also highly correlated. This indicates that spiders take-off, balloon and land within the same short period of time. In the present study more spiders were ballooning close to the ground than at 12.2 m, indicating that most spiders were not lifted very high on air currents. Traditionally, it has implicitly been assumed that spiders balloon by a few long flights (e. g., Greenstone et al. 1987; Greenstone 1991; Sunderland & Topping 1993; Toft 1995). However, it has recently been proposed that spiders in general balloon by many short flights, often only travelling a few meters per flight (Topping et al. 1992; Thomas 1992). Thus, during an aerial dispersal event, a spider will take-off, balloon some distance and land, then repeat this process until it has found a suitable habitat or as long as weather allows ballooning (Tolbert 1977; Heidger & Nentwig 1989). If ballooning is mostly by a few long flights, then BI would measure mainly emigration, and deposition traps would measure mainly immigration. However, if spiders balloon by many short flights, then BI, suction traps, sticky traps and deposition traps will all catch a combination of spiders taking-off and spiders landing, and spiders leaving, entering or just passing through/over the habitat cannot be

separated. The data presented here suggest that the majority of aerially dispersing spiders make a number of short-duration flights, as more spiders were consistently caught in the 1.4 m suction trap than in the 12.2 m trap. This was consistent throughout the year, i. e., no seasonal change in the ratio of numbers caught at 1.4 m and 12.2 m, indicating that the seasonal changes in height distribution and distance travelled, suggested by Toft (1995) for Denmark, do not apply in UK. Hence, spiders would also be able to re-colonize fields in winter. However, the distance that a spider can disperse in a day will depend both on the distance of flights and on how long the climatic conditions allow re-ballooning. Our data suggest that spiders balloon fewer hours per day during autumn than spring and summer.

To help researchers to select an appropriate method for their own circumstances we here compare the man-hours and costs needed for BI, suction traps, deposition traps and sticky traps. BI takes 5 min per observation and a minimum of four observations a day, so in total it would take 2h 20 min/week. However, this can be greatly reduced if observations are only carried out at wind speeds below 3.5 m/s. The costs of materials are negligible (below US \$5). Suction trap samples take around 15 min to collect and count, in total 1 h 45 min/week. The cost of the 1.4 m Propeller Suction Trap is approx. US \$1600 and US \$3900 for the 12.2 m Rothamsted Insect Survey Trap. The water traps used by Topping and Sunderland (1995) took on average 1 hour per trap to sort and count, however during summer this may be up to three hours per sample. Topping and Sunderland (1995) used 6 traps, which took 6–12 h/week. The deposition traps used by Topping and Sunderland (1995) were fairly expensive (approx. US \$80 per trap), but a simpler and cheaper design could be used. Sticky traps would take approximately the same time to process as water traps with the same sampling effort. However, in summertime they do get clogged quickly and have to be changed at shorter intervals. Materials would cost approximately US \$10 per trap per week.

In conclusion, the pre-ballooning activity measured by BI corresponded well with aerial density measured by suction traps (especially when considering the very different mecha-

nism of BI and suction traps, the large difference in sampling effort and variation in timing of observations for BI). Hence, BI appears to be a robust and useful method for measuring aerial dispersal activity of spiders. It uses inexpensive equipment and its total cost will be very low if the array of sticks can be sited close to a laboratory or a frequently-manned field station. If, however, the array is set up in a remote location, then travel and labor costs have also to be taken into account when deciding whether to use BI or a more automatic system (such as a suction trap emptied at weekly intervals).

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A TEST FOR REPRODUCTIVE SEPARATION OF ALTERNATE GENERATIONS IN A BIENNIAL SPIDER, *ARANEUS DIADEMATUS* (ARANEAE, ARANEIDAE)

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ABSTRACT. In Denmark, two seemingly distinct size-classes, 3rd and 4th instar juveniles and reproductive adults, of *Araneus diadematus* are found during every breeding season in autumn, indicating a non-overlapping biennial life-cycle. We tested the hypothesis that alternate generations might experience a degree of reproductive isolation, using the distribution of nuclear (allozyme) and maternal (mtDNA) genetic markers. Individuals of a locality behaved as belonging to a random mating population, irrespective of size. No differences were found between any size-class pairs, within and between 2 yr, or among geographically distant samples. Processes that may lead to this result are discussed: the biennial development may be incomplete; or there may be migrational influx of genes from southern annual populations. There is no evidence for sexual differences in life-cycle length.

Keywords: Araneae, life history, biennial reproduction, mitochondrial DNA, allozymes

Several species of spiders at northern latitudes need an extended time to reach sexual maturity compared to their more southern conspecifics (Toft 1976 and references therein). The ecological background promoting such a life-cycle shift may result from lower temperature and shorter seasonal length (Roff 1992). Life-cycle shifts may also be viewed as a strategy to maximize fecundity by avoiding intraspecific competition (Polis 1984; Roff 1992). Most recorded life-cycle shifts in spiders involve species that extend their annual life-cycle in south and central Europe to a biennial life-cycle in northern Europe (Almquist 1969; Toft 1976). If the biennial development is perfect, cohorts that mature in even and uneven years will never mix. Dividing conspecifics into separately reproducing cohorts can foster sympatric race formation and, ultimately, speciation. In this manner, the 13-yr and 17-yr periodical cicadas have evolved into distinct evolutionary units (Archie et al. 1985; Marshall 2000).

The life-cycle of *Araneus diadematus* Clerck 1757 is generally described as annual (Bonnet 1930). However, in northern regions of Europe *A. diadematus* needs two years to

reach sexual maturity (Toft 1976). In Denmark, *A. diadematus* reaches maturity in July–August and mates through August and early September. The females lay a single egg sac in October. The egg sac overwinters, while the parent generation disappears before winter. Reproduction in spring has never been observed. In the breeding season two seemingly distinct size-classes can be observed: ca. 3rd to 4th instar juveniles (i.e., young of previous year's reproduction) and sexually mature animals (two years old). This pattern has consistently been observed during the past 30 years (Toft 1976; Toft pers. obs.). Analysis of size structure in the field produced no evidence for different developmental patterns in males and females (Toft 1976). It seems as if populations of *A. diadematus* have split into two non-overlapping cohorts.

The combination of a narrow breeding season and the repeated annual occurrence of two distinct size classes led us to speculate whether *A. diadematus* experiences some degree of reproductive isolation, i.e., whether size classes constitute two discontinuous cohorts. We tested reproductive separation assuming two hypotheses. First, reproductive separation can

be estimated as a departure from random mating between cohorts. This leads to the well-known Wahlund-effect (Wahlund 1928). Furthermore, given a 2-yr life-cycle, juveniles of a certain year should correlate genetically with adults of the following year, relative to adults of the same year. The same reasoning holds for adults of a certain year and juveniles of the next year. Second, a sex-specific developmental cycle is possible (cf. Levy 1970) though it seems to be rare, at least in temperate species (Schaefer 1987). If, for example, females mature in 2 years and males in 1 year, no differentiation of allozyme frequencies would be possible. However, if females' biennial development is complete, mtDNA might possibly have diverged. We tested this hypothesis using maternally inherited mitochondrial DNA.

METHODS

Juvenile (3rd and 4th instars) and adult spiders were collected at Mols, Denmark in the autumn of 1998 and 1999 (M98-J(uvenile), M98-A(dult), M99-J, M99-A) and from the 300 km distant island of Bornholm, near Hammern, in 1998 (H98-J, H98-A). Each size-class, at each location, was treated as a sample. All collections were done in the month of September, i.e., at a time when all the breeders of the year had matured. Bornholm is an isolated island in the Baltic Sea, approximately 30 km southeast of Sweden and 80 km north of Poland. The Bornholm samples were used to analyze the influence of geographic distance relative to genetic divergence between size groups, under the rationale that if two distinct reproductive groups exist, then correlations within size-groups should be independent of geographic distance.

All cohort related hypotheses were tested by applying biparental inherited markers (allozymes) and maternally inherited markers (mitochondrial DNA). Nine polymorphic loci, could be constantly scored in all samples: *Aat-2* (E.C. 2.6.1.1), *Fum* (E.C. 4.2.1.2), *Gpd* (E.C. 1.1.1.8), *Idh-1*, -2 (E.C. 1.1.1.42), *Pgd* (E.C. 1.1.1.44), *Mpi* (E.C. 5.3.1.8), *Pgi* (E.C. 5.3.1.9), *Pgm* (E.C. 5.4.2.2). The locus *Adh* (E.C. 1.1.1.1) was also polymorphic but stained too weakly for juveniles to be analyzed, and was omitted from further analysis.

Electrophoretic analysis was done by cellulose acetate electrophoresis (Hebert & Bea-

ton 1993). A total of 121 spiders were investigated (see Table 1). Three buffer systems were used: Tris-Maleic acid pH = 7.0 (Richardson et al. 1986, adjusted with maleic acid to pH = 7.0 from pH = 7.8) for *Aat-2*, *Mpi*, *Pgd*. Tris-Citrate pH = 8.2 (Richardson et al. 1986) for *Gpd*, *Pgi*, *Idh*. Tris-Glycine pH = 8.5 (Hebert & Beaton 1993) for *Adh*, *Fum*, *Pgm*. All enzymes were run at 250V for 30 min.

Departure from random mating among juveniles and adults was tested as a departure from Hardy-Weinberg proportions for all spiders collected at Mols in the years 1998 and 1999, respectively, with the program GENEPOP (Raymond & Rousset 1995a). Differentiation among samples was quantified using the F_{ST} estimator of Weir & Cockerham (1984). F_{ST} is defined between 0 and 1, where $F_{ST} = 0$ signifies no variance among samples and $F_{ST} = 1$ signifies that all variance is distributed between samples. F_{ST} -analyses are based on allele frequencies summed over all loci. Divergence initially may proceed at a single locus, e.g., under selection, before genetic drift leads to divergent allele frequencies at other loci (e.g., McKechnie et al. 1975; Johannesson et al. 1995). Therefore, we tested for allele frequency homogeneity at each locus between all population pairs using exact tests (Raymond & Rousset 1995b) with GENEPOP. The relationship among juveniles and adults, and geographic locations was investigated applying maximum likelihood analysis with the program package PHYLIP (Felsenstein 1993). This algorithm assumes divergence by genetic drift only. Branch lengths are relative to divergence, and each is tested for significance.

Finally, we sequenced the mitochondrial DNA gene ND1 for 580 base pairs. ND1 has proven to be highly variable in other species of spider (Hedin 1997; Croucher 1998; Johannessen & Veith in press, Johannessen pers. obs.). Initially, two individuals from H98-J, and three individuals from all other samples were analysed, $n_{tot} = 17$. Amplification protocol and ND1 primers can be found in Hedin (1997). DNA fragments were sequenced in both directions. Sequences were aligned using the program Sequence Navigator and successively checked manually.

Table 1.—Allele frequencies at nine polymorphic loci for *A. diadematus*. For locality abbreviations please refer to the text.

		M98-J	M98-A	M99-J	M99-A	H98-J	H98-A
<i>Fum</i>	1	0.85	0.90	0.89	0.85	0.80	0.70
	2	0.15	0.10	0.11	0.15	0.20	0.30
<i>Aat-2</i>	1	0.96	0.96	0.92	1.00	1.00	1.00
	2	0.04	0.04	0.08	0	0	0
<i>Gpd</i>	1	0.21	0.27	0.13	0.25	0.15	0.07
	2	0.02	0	0	0	0	0
	3	0.77	0.73	0.87	0.75	0.85	0.93
<i>Idh-1</i>	1	0.81	0.81	0.92	0.90	0.80	0.91
	2	0.19	0.19	0.08	0.10	0.20	0.09
<i>Idh-2</i>	1	0.04	0.04	0	0	0.17	0
	2	0.96	0.96	1.00	1.00	0.83	1.00
<i>Pgd</i>	1	0	0	0.13	0.03	0	0.04
	2	0	0	0.05	0	0	0
	3	0.98	1.00	0.79	0.93	0.90	0.89
	4	0.02	0	0.03	0.05	0.10	0.07
<i>Pgi</i>	1	0.02	0.02	0.05	0.03	0	0.04
	2	0.62	0.40	0.53	0.53	0.40	0.50
	3	0.25	0.44	0.34	0.26	0.45	0.35
	4	0	0.04	0	0	0.10	0
	5	0.12	0.10	0.08	0.18	0.05	0.11
<i>Pgm</i>	1	0.02	0	0	0	0	0
	2	0.87	0.90	0.87	0.77	0.85	0.87
	3	0.12	0.10	0.13	0.22	0.10	0.13
	4	0	0	0	0	0.05	0
<i>Mpi</i>	1	0	0	0.04	0.06	0.09	0.02
	2	0.65	0.26	0.54	0.63	0.50	0.50
	3	0.31	0.52	0.32	0.31	0.41	0.35
	4	0.04	0.22	0.11	0	0	0.13
	N	26	24	19	20	10	22

RESULTS

Only a single mtDNA haplotype, thus no mtDNA differences among samples, was observed (Genbank number AY036084). We did not sequence further individuals after this result.

The allozyme allele frequencies are shown in Table 1. There were no allozyme-genetic correlations between alternate generations, nor were there deviations from Hardy-Weinberg proportions among generations within the same year at the same locality, $P > 0.50$. No allozyme differentiation was found among all samples, $F_{ST} = 0.018 \pm 0.013$, and no internal branches of the maximum likelihood phenogram were significantly greater than zero (tree not shown). No among-sample allele frequency differences were found in the loci *Pgi*, *Pgm*, *Idh-1*, *-2*, *Aat* and *Fum*. For the loci *Mpi*, *Pgd*, and *Gpd* allele number differences

were found for a single deviating sample, relative to all other samples.

Thus, neither hypothesis could be confirmed. There were no genetic differences between juveniles and adults of the same year, no genetic correlations between alternate generations, and no differences among females from different years. Furthermore, there were no genetic differences between geographically distant samples.

DISCUSSION

This study was inspired by the notion that the recurrent appearance in autumn of two size classes of *A. diadematus*, coupled to its narrow breeding season, could be related to reproductively separated cohorts. However, a lack of differentiation among samples was observed for nuclear genetic markers and no variation was observed in maternally inherited

mtDNA markers. No correlations between size classes or sexes were found. Thus, the genetic markers were not able to separate the size groups into two reproductive cohorts.

A lack of genetic correlation does not prove that *A. diadematus* size-classes are, to some extent, reproductively isolated. Lack of genetic correlations can be a consequence of large population sizes that cause genetic drift to have little power in separating cohorts. However, genetic homogeneity at nine allozyme loci suggests that cross-generation matings may not be uncommon. It is unlikely that too-small sample sizes resulted in a lack of significant correlations because alleles of the most polymorphic loci, where the sample error should be greatest, were all homogeneously distributed. It is more likely that the biennial life-cycle of *A. diadematus* is not complete, i.e., that a small fraction of the population (and probably both sexes) cross the generations by having annual or triannual life-cycles. Such mixed life-cycles are well known in several species of spiders (Toft 1976, 1983), but they are recognized easily only by standard analysis of size distributions if the developmental lines are numerically well represented. More extensive sampling or laboratory breeding studies may elucidate this possibility.

Uniform distributions of allozyme alleles from two locations 300 km apart indicated that gene flow may occur over large distances. High mobility by ballooning (Foelix 1996) is a possible reason for lack of differentiation both between the geographically distant samples (Ramirez & Haakonsen 1999) and between alternate cohorts. Furthermore, especially for mtDNA, lack of variation may be influenced by post-glacial colonization due to founder events. Colonization is not expected to influence the variation of nuclear genes as much because the effective population size of nuclear genes is four fold that of mtDNA. The level of allozyme polymorphism in *A. diadematus* is similar to that found in other spiders examined in northern Europe. These studies were able to separate local populations (Pedersen & Loeschcke 2001; Johannesen & Veith 2001) and even delimit micro-structures within populations (Johannesen et al. 1998; Schäfer et al. 2001).

In the face genetic homogeneity, caused either by gene flow or a recent life history split,

the recurrent occurrence of two size classes suggests strong selection for maintaining biennial life cycles. The phenomenon of divergence of biennial northern and southern annual populations remains an intriguing question. Immigration from central populations is thought to impede genetic adaptations of peripheral populations (Hoffmann & Blows 1994). Given a high dispersal potential, it is possible that immigrants from southern populations with an annual life-cycle can hinder separation of distinct cohorts, in that mobility among populations will break down any sign of intra-population cohort divergence. Therefore, the question arises about the extent of dispersal mobility of *A. diadematus*.

Reports on ballooning activity of *A. diadematus* are few and inconclusive. During analysis of seven year's catches by a 12.2 m high Rothamsted suction trap near Copenhagen, Denmark, Toft (pers. obs.) found four individuals, all 3rd or 4th instar juveniles. Three were captured in August–October of their first year, and one in June of the second year. Animals that are caught in this trap are assumed to be long-distance dispersers, because the catch is independent of the immediate surroundings of the trap due to its height. Though the number trapped is rather low, the data suggest that dispersal is predominantly in medium-sized instars, in which both autumn and spring dispersal is possible. Relatively, ballooning activity may be higher than the figures seem to indicate if related to the populations on the ground. *Araneus diadematus* is a widespread species, but it occurs only locally in high densities. It may thus be sufficiently active as a balloonier to explain the lack of geographical differentiation. The zone of transition between annual and biennial life-cycle of *A. diadematus* is unknown but may be only a few hundred kilometres south of Denmark. Even if it is unlikely that the distance may be bridged regularly by single individuals, accumulated dispersal over some generations may create the gene flow necessary to prevent genetic divergence of alternate biennial generations, even if there are no local “cross-overs” between alternate generations. In conclusion, we suggest that both intra- and inter-population gene flow may play a role in preventing intra-population differentiation.

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ESTIMATION OF CAPTURE AREAS OF SPIDER ORB WEBS IN RELATION TO ASYMMETRY

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ABSTRACT. We examined the utility of several popular formulae used to estimate the capture areas of orb webs across a large sample of *Cyclosa* Menge 1866 and *Tetragnatha* Latreille 1804 webs. All formulae evaluated contained at least some bias in estimation of the capture areas of webs. We identified two types of asymmetry in orb webs that affect capture area estimation differently. Web asymmetry measures the ratio of the horizontal and vertical diameters of orb webs while hub asymmetry measures the displacement of the hub from the geometric center of a web. An analysis of model webs that varied in web and hub asymmetry showed that most formulae overestimated capture area as web asymmetry increased and that some formulae also overestimated capture area as hub asymmetry increased. Only the “Ellipse–Hub” formula was unaffected by web and hub asymmetry. Although the “Adjusted Radii–Hub” formula provided a slightly more accurate overall estimate of capture area, we recommend that the “Ellipse–Hub” formula be used when comparisons of capture area are made between taxa or individuals that vary in web and hub asymmetry.

Keywords: Web architecture, asymmetry, sticky silk, capture spiral, spider web

Orb-weaving spiders provide excellent models for the study of a variety of questions in behavior and ecology because measurement of the architectural features of webs allows us to quantify and compare many aspects of spider behavior. The sizes and shapes of webs can directly influence both the foraging success and predation risk of spiders (Rypstra 1982; Eberhard 1986; Higgins 1992; Blackledge & Wenzel 1999, 2001). Spiders also actively modify the architectures of webs in response to predators and prey (Higgins & Buskirk 1992; Pasquet et al. 1994; Sherman 1994; Vollrath et al. 1997; Blackledge 1998). Thus, studying architectures of spider webs can give us insight into how spiders confront selective pressures in their environment.

Some aspects of webs can be difficult to measure accurately in the field so that formulaic estimators are instead employed (Heiling et al. 1998; Herberstein & Tso 2000; Venner et al. 2001). For instance, the total area of a web, as delimited by the outermost sticky spiral, or the capture area of a web (total area—the central non-sticky free zone and hub) are often used as indicators of the foraging effort of a spider but cannot be mea-

sured directly in the field (Sherman 1994; Tso 1996; Blackledge 1998; Herberstein et al. 2000). Some studies have used single radial measurements or circular approximations to estimate web or capture area from field measurements (McReynolds & Polis 1987; Higgins & Buskirk 1992). But, most orb webs have an elliptical shape and an asymmetric placement of the central hub so that capture areas are estimated poorly by simple circular approximations (ap Rhisiart & Vollrath 1994; Herberstein & Heiling 1999; Herberstein & Tso 2000).

Herberstein & Tso (2000) recently examined the accuracy of several formulae used to estimate the capture areas of webs. They used linear regression to compare the capture areas estimated by four formulae and the actual capture areas of 11 *Argiope keyserlingi* Karsch 1878 webs. Herberstein & Tso found that estimates from the “Adjusted Radii–Hub” formula were most correlated with the actual capture areas of webs, and they argued that the “Adjusted Radii–Hub” formula provided the best estimator of capture area in part because it accounted for web asymmetry. However, to date there has been no assessment of

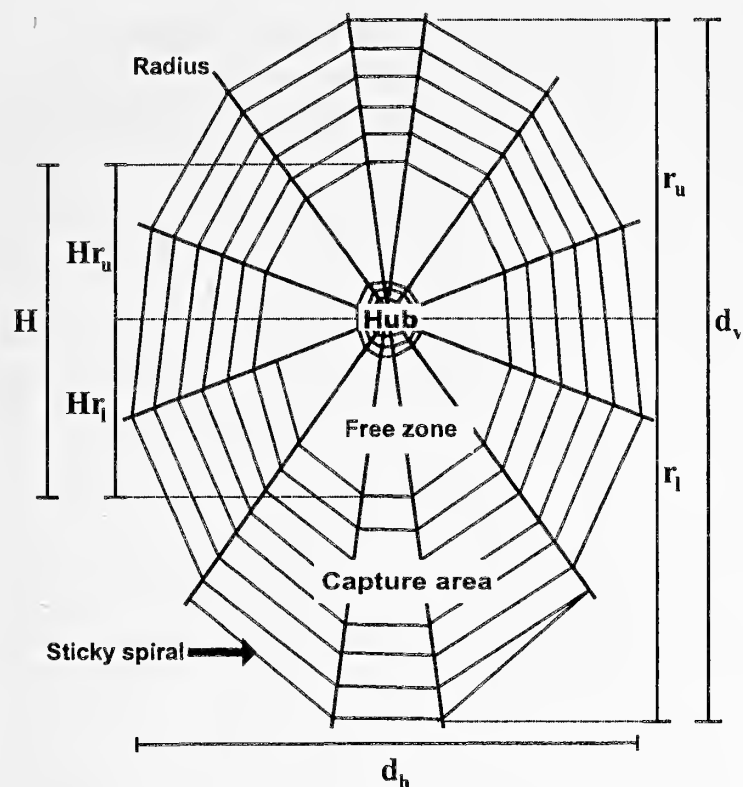


Figure 1.—Orb web illustrating the parameters measured for each of the capture area estimation formulae in Table 1. The outermost spiral of sticky silk delimits total web area. The hub is the innermost portion of the web, where the spider rests, and has a non-sticky hub spiral. The free zone is devoid of a spiral. Capture area is the portion of the web delimited by the innermost and outermost sticky spirals of capture silk. Web asymmetry is a measure of the ratio of the horizontal and vertical diameters of the web $[1 - (d_h/d_v)]$. Hub asymmetry is a measure of the vertical displacement of the hub from the geometric center of the web $[1 - (r_u/r_l)]$. This web has a web asymmetry of 0.27 and a hub asymmetry of 0.26.

the utility of any of these formulae across multiple taxa of spiders even though different species of spiders vary greatly in web architecture. Nor has there been any systematic study of the effects of web or hub asymmetry on the performance of these formulae.

We examine the performance of four capture area estimation formulae, used in the current literature and examined by Herberstein & Tso (2000), for a large sample of *Cyclosa* (Araneidae) and *Tetragnatha* (Tetragnathidae)

webs. The webs built by these two genera can be quite different from one another and represent a fairly broad range of the interspecific variation to be found in architectural features of orb webs. *Cyclosa* tend to build webs that are under high tension, have large numbers of radii and long sticky spirals, and are relatively asymmetric, while *Tetragnatha* webs tend to be under lower tension, have fewer radii and shorter sticky spirals, and are more symmetric (see Fig.1 and Zschokke 1999 for definitions of orb-web nomenclature).

METHODS

We photographed webs in the field during a 2 mo study of the diversity of Hawaiian orb-weaving spiders, represented exclusively by *Cyclosa* and *Tetragnatha*. Spiders were collected from webs. Webs were then dusted with cornstarch to improve visibility of silk and photographed using a Nikon SLR camera. Only a single web was photographed per spider. Our sample includes multiple individuals for each species and approximately a dozen species for each genus. But our comparison in this study is restricted to that between *Cyclosa* and *Tetragnatha*. We measured the vertical and horizontal diameters of webs in the field to provide scaling factors (d_v and d_h in Fig. 1). Photographs were digitized and analyzed on a Microsoft Windows computer using the Scion Image program (ported from NIH Image for the Macintosh by Scion Corporation and available on the Internet at <http://www.scioncorp.com>). Using the digital image, we measured the actual capture areas of webs as delimited by the innermost and outermost sticky spirals and all of the parameters necessary to calculate each of the capture area estimation formulae examined by Herberstein & Tso (see Fig.1 and Table 1). All measurements were scaled using the field measurements of web diameters.

We also calculated two types of asymmetry in the architectures of webs. The term web

Table 1.—Capture area estimation formulae examined in Herberstein & Tso (2000).

Vertical Radii - Hub	$(d_v/2)^2\pi - (H/2)^2\pi$
Tso - Hub	$[\frac{1}{2}\pi r_u^2 - \frac{1}{2}\pi(H/2)^2] + [\frac{1}{2}\pi r_l^2 - \frac{1}{2}\pi(H/2)^2]$
Ellipse - Hub	$(d_v/2)(d_h/2)\pi - (H/2)^2\pi$
Adjusted Radii - Hub	$[\frac{1}{2}\pi r_{au}^2 - \frac{1}{2}\pi(H_r_u)^2] + [\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi(H_r_l)^2]^*$

* $r_{au} = (r_u + d_h/2)/2$ and $r_{al} = (r_l + d_h/2)/2$.

asymmetry has been used by previous investigators to refer to a disparity in the amount of silk or area of a web above the hub compared to that below the hub (e.g. ap Rhisiart & Vollrath 1994; Herberstein & Heiling 1999). Increase in web asymmetry is often assumed to be synonymous with an increase in the elliptical shape of webs. But the overall shape of a web and placement of the hub can vary independently, so that there are two separate types of asymmetry in orb webs. Here, we define “web asymmetry” as the departure of the outermost spiral of sticky silk of an orb-web from a circular shape, calculated as:

$$\text{web asymmetry} = 1 - d_h / d_v$$

Thus, a perfectly circular web has a web asymmetry of 0 while most webs have asymmetry values slightly > 0 . Occasionally, webs will have negative web asymmetries. “Hub asymmetry” measures displacement of the hub from the geometric center of the web, regardless of the overall shape of the web. It is calculated as:

$$\text{hub asymmetry} = 1 - r_u / r_l$$

Most webs have hub asymmetry values slightly > 0 , while the hub asymmetry of a web with the hub in the geometric center = 0.

All four capture area estimation formulae that we consider calculate an estimate of the total area of a web, measured from the outermost spiral of sticky silk, and then subtract a circular approximation of the area of the free zone and hub to calculate the remaining area of the web, which is covered by capture silk (see Fig. 1 and Table 1). The “Vertical Radii–Hub” formula provides a simple circular approximation for total web area, using only a single vertical diameter distance each for the total web (d_v) and hub (H) areas respectively (Brown 1981; McReynolds & Polis 1987; Higgins & Buskirk 1992 all use single geometric radial measurements as indices of web area). The “Tso–Hub” formula treats the upper and lower halves of a web as separate semi-circles, estimating areas of each semi-circle based upon a single measurement of a geometric radius each (r_u and r_l ; Tso 1996). These radii (r_u and r_l) are measured from the hub of the web and will therefore vary with changes in hub asymmetry even when web asymmetry remains constant. The “Ellipse–Hub” formula is the only formula that

uses an elliptical, rather than circular, approximation of total web area, based upon both horizontal and vertical geometric radial distances (Miyashita 1997; Blackledge 1998; Watanabe 1999). The “Adjusted Radii–Hub” formula is a modification of the “Tso–Hub” formula that computes geometric radial distances from the average of both the horizontal and vertical geometric radial distances, for both the lower and upper half of the web (Table 1; Herberstein & Tso 2000). The “Vertical Radii–Hub” and “Ellipse–Hub” formulae calculate geometric radial distances from the geometric center of the web by halving the diameter of the web, which does not vary with hub asymmetry. The “Tso–Hub” and “Adjusted Radii–Hub” formulae measure geometric radial distances from the hub of the web so that these measurements will vary with changes in hub asymmetry.

After estimating capture areas of webs using each formula, we followed the example of Herberstein & Tso (2000) and used linear regression to examine the relationship between the actual and estimated capture areas of webs. Herberstein & Tso (2000) found that, for *Argiope keyserlingi*, the accuracy of formulae varied by up to 60%. They suggested that some of the differences in accuracies of capture area estimations were due to differences in the abilities of each formula to account for the elliptical shapes of webs. But, Herberstein & Tso (2000) did not specifically examine how accuracy of those formulae was affected by web asymmetry. They also did not examine the impact of hub asymmetry on performance of the “Tso–Hub” and “Adjusted Radii–Hub” estimators. Therefore we performed a second set of regression analyses examining the correlation between error generated by each estimator and web and hub asymmetry. We calculated the % error generated by each estimate as:

$$(\text{estimated capture area} - \text{measured capture area}) * 100 / \text{measured capture area}$$

Finally, we used each formula to estimate the areas of a series of model webs. We generated ellipses that varied in shape from a perfect circle to model webs that had 10 and 20% greater vertical diameters than horizontal diameters (web asymmetry values of 0, 0.09, and 0.17 respectively). For each of these web asymmetry values we also varied hub asym-

Table 2.—Mean estimated capture area and regression of measured capture area versus estimated capture area for each of four different formulae. *n* = 226.

Estimator	Mean ± SE (cm ²)	Functional relationship	<i>F</i> _{1,225}	<i>P</i>	Adjusted <i>R</i> ²
Measured area	164.0 ± 7.4				
Vertical Radii - Hub	214.3 ± 11.3	<i>y</i> = −14.2 + 0.91 <i>x</i>	1090.8	<0.00001	0.829
Tso - Hub	222.2 ± 12.6	<i>y</i> = −26.4 + 0.89 <i>x</i>	810.9	<0.00001	0.783
Ellipse - Hub	151.6 ± 6.8	<i>y</i> = 3.2 + 0.99 <i>x</i>	7251.0	<0.00001	0.970
Adjusted Radii - Hub	159.8 ± 7.4	<i>y</i> = −1.42 + 0.95 <i>x</i>	4499.9	<0.00001	0.952

metry from model webs where the hub was at the geometric center to model webs where hubs were 10 and 20% closer to the tops (hub asymmetry values of 0, 0.18, and 0.23 respectively). This analysis controlled for error generated when real spider webs are not perfectly elliptical in shape as well as any effects of measurement error with the experimental webs. Therefore, any error in estimation of capture area of these model webs is due solely to the effects of web and hub asymmetry.

RESULTS

The “Adjusted Radii–Hub” formula gave the closest mean estimate of capture area to that of the actual capture area, but its mean estimate did not differ significantly from that of the “Ellipse–Hub” formula (Table 2). The “Ellipse–Hub” formula was slightly more correlated with variation in the actual capture areas of webs (see *R*² in Table 2). Both of these formulae tended to underestimate capture areas of webs (Table 2). In contrast, the “Vertical Radii–Hub” and “Tso–Hub” formulae both greatly overestimated sizes of webs and were about 20–25% less correlated with actual capture areas (see *R*² in Table 2). For larger webs, all formulae, except the “Ellipse–Hub” formula, tended to give higher estimates for the capture areas of *Cyclosa* webs than for *Tetragnatha* webs (Fig. 2).

Web asymmetry was greater for *Cyclosa* (mean ± SE = 0.24 ± 0.02) than for *Tetragnatha* (mean ± SE = 0.13 ± 0.02). Hub asymmetry of webs was also higher for *Cyclosa* (mean ± SE = 0.28 ± 0.02) than *Tetragnatha* (mean ± SE = 0.09 ± 0.02). Web and hub asymmetry were largely uncorrelated with one another (*R*² = 0.02; Fig. 3).

Over 90% of the error in estimation of capture areas could be explained by variation in web and hub asymmetry when using the

“Vertical Radii–Hub” and “Tso–Hub” formulae (Table 3). Web and hub asymmetry also explained 20% of the variation in estimation error generated by the “Adjusted Radii–Hub” formula. But web asymmetry and hub asymmetry was uncorrelated with error from the “Ellipse–Hub” formula and hub asymmetry explained only 5% of the variation of the total error generated by the “Ellipse–Hub” formula.

Analysis of model webs showed that all formulae gave perfect estimates when there was no web or hub asymmetry (i.e. when web shape was a perfect circle; Fig. 4). Error increased with increasing web asymmetry for all formulae except the “Ellipse–Hub” formula. Error also increased as hub asymmetry increased for the “Tso–Hub” and “Adjusted Radii–Hub” formulae. Overall, the “Vertical Radii–Hub” and “Tso–Hub” formulae generated much larger errors, an order of magnitude larger than the “Adjusted Radii–Hub” formula. The “Ellipse–Hub” generated no error in the estimation of capture areas of model webs as web or hub asymmetry changed.

DISCUSSION

We found that the “Adjusted Radii–Hub” formula of Herberstein & Tso (2000) produced a mean estimate of capture area of webs that was closest to the mean of the actual measured values, but that capture area estimates from the “Ellipse–Hub” formula were more correlated with measured capture areas of individual webs (Table 2). Both the “Vertical Radii–Hub” and “Tso–Hub” formulae performed much worse, giving mean estimates of capture area that were approximately 30% greater than the mean of the measured capture area. Estimates from the “Vertical Radii–Hub” and “Tso–Hub” formulae were also about 20% less correlated with measured

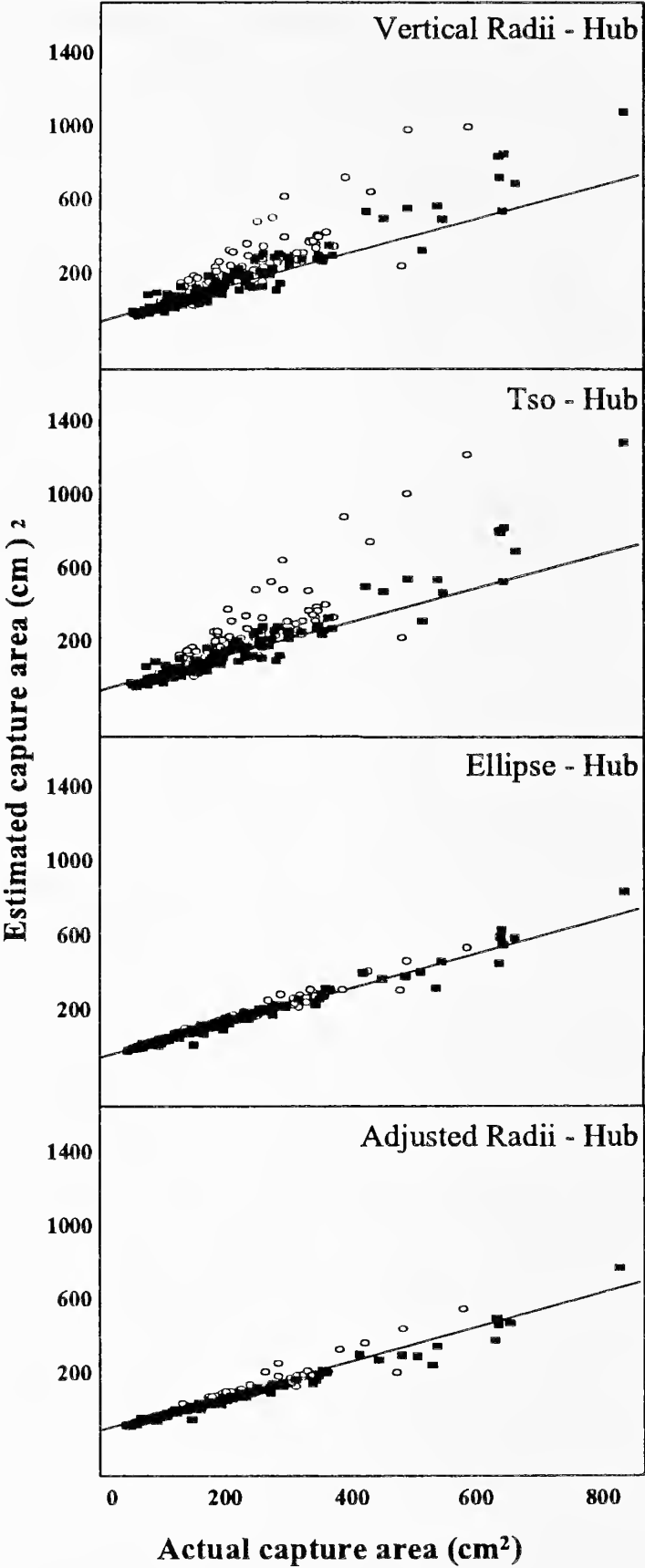


Figure 2.—Relationships between capture area estimates and actual capture areas of webs for each of four formulae. Lines denote perfect correlations. ■ = *Tetragnatha*, ○ = *Cyclosa*.

capture area compared to estimates from the “Ellipse–Hub” and “Adjusted Radii–Hub” formulae (Table 2).

Our analysis of model webs gives an explanation for much of the error generated by capture area estimation formulae. The analysis demonstrates that all formulae except for the “Ellipse–Hub” formula give biased estimates

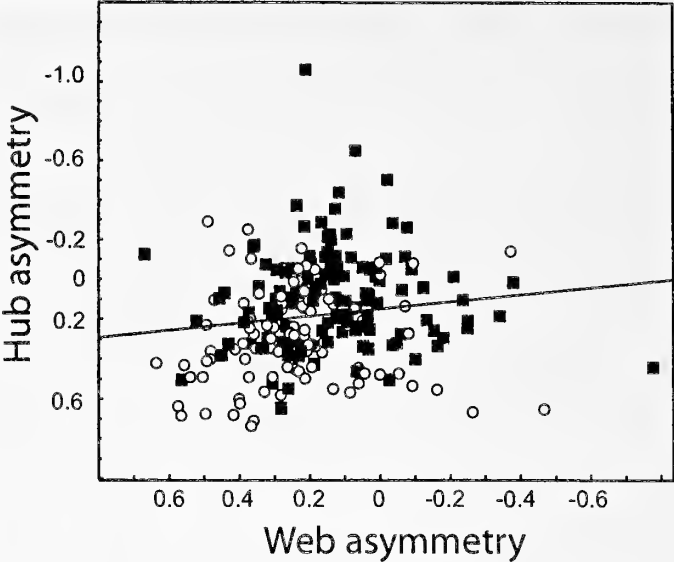


Figure 3.—Hub and web asymmetry can vary independently of one another in webs ($R^2 = 0.02$). ■ = *Tetragnatha*, ○ = *Cyclosa*.

as web asymmetry increases (Fig. 4). The “Vertical Radii–Hub” and “Tso–Hub” formulae give gross over-estimates of the capture areas of elliptical webs because their circular approximations of web area use only vertical measurements when calculating area. The “Adjusted Radii–Hub” formula performs better because it calculates an average distance based upon both vertical and horizontal measurements. Yet, the “Adjusted Radii–Hub” formula still generates some error with increasing web asymmetry because its estimation is based upon approximating capture area as two semi-circles, rather than a single ellipse, even when a web has an elliptical shape. The “Tso–Hub” and “Adjusted Radii–Hub” formulae have a second source of bias. The error of both estimators also increases with hub asymmetry, even when capture area is constant (Fig. 4). This error occurs because both of these formulae calculate radial measures from the center of the hub of the web rather than the geometric center of the web. As hub asymmetry increases the semi-circular estimate of the capture area of the lower halves of webs greatly overestimates capture area, while capture area of the upper halves of webs is underestimated. Because most of the capture areas of webs with high hub asymmetry is in the lower half, the overestimation of area in the lower halves of webs overshadows the underestimation of areas in the upper halves of webs resulting in a net overestimation of web capture area.

These findings from model webs largely agree with our data from real webs. Error was

Table 3.—Regression of the error of capture area estimates on web (x) and hub (z) asymmetry. Web and hub asymmetry were significant predictors of error for all formulae, except the “Ellipse – Hub” estimator for which only hub asymmetry was significant.

Estimator	Functional relationship	$F_{2,224}$	P	Adjusted R^2
Vertical Radii – Hub	$y = 1.1 - 0.94x$	970.6	<0.00001	0.90
Tso – Hub	$y = 1.3 - 0.87x - 0.23z$	1120.6	<0.00001	0.91
Ellipse – Hub	—	2.6	N.S.	0.02
Adjusted Radii – Hub	$y = 0.2 - 0.31x - 0.33z$	37.4	<0.00001	0.25

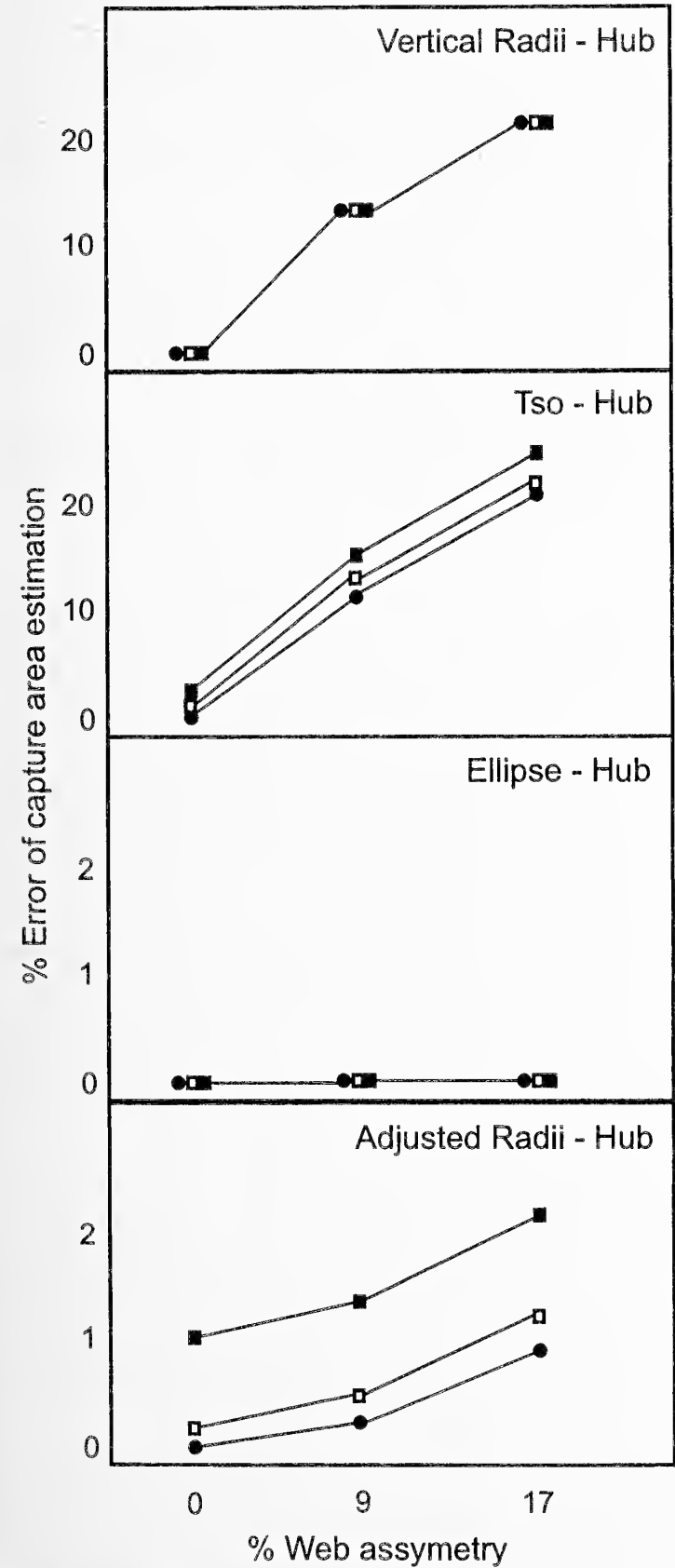


Figure 4.—Error generated by formulae when estimating capture area of model webs of perfect elliptical shape that vary in web and hub asymmetry. Hub asymmetry: ● = 0%, □ = 18%, and ■ = 23%.

strongly related to both web and hub asymmetry for the “Tso–Hub” formula ($R^2 = 0.99$, Table 3). Web asymmetry also explained much of the variation in error from the “Vertical Radii–Hub” formula ($R^2 = 0.90$, Table 3). Unexpectedly, hub asymmetry was also a significant predictor, although its slope in the regression analysis was much smaller than for web asymmetry indicating that hub asymmetry accounted for much less of the variability in error ($\beta = 0.86$ and 0.12 respectively). Both web and hub asymmetry were also correlated with the error generated by the “Adjusted Radii–Hub” formula, but explained relatively less of the error generated by this formula ($R^2 = 0.19$, Table 3). An additional source of error for all formulae can be explained by the extreme reduction in sticky silk in the upper portions of some webs. Especially for spiders such as *Cyclosa* (pers. obs.) or *Nephilengys* (Edmunds 1993) that sometimes build webs with little or no sticky silk above the hub, webs with extreme hub asymmetry can assume a semi-circular, rather than elliptical, shape that cannot be accurately estimated by any of the formulae. Thus, departure from an elliptical shape by some orb webs is a third important source of error when estimating capture area, although our study gives no evidence to suggest whether formulae differ in their ability to account for oddly shaped webs. A final source of error is that introduced by researchers when making the measurements of parameters necessary to use each formula. Although we did not examine how this varies between formulae, we expect this source of error to be greater for formulae that require more parameters.

Overall, the performance of the “Vertical Radii–Hub” and “Tso–Hub” formulae were so poor that we recommend they not be used. The “Adjusted Radii–Hub” gave a slightly more accurate estimation of capture area than

the “Ellipse–Hub” formula when averaged across all webs, but its precision was slightly worse (Tables 2 & 4, total range of errors was –39 to +56% and –21 to +58% respectively). The “Adjusted Radii–Hub” formula had a lower mean error because it tended to underestimate areas of symmetric webs but overestimated capture area when web and hub asymmetry were high resulting in a low net error, while the “Ellipse–Hub” formula consistently underestimated capture areas of all webs slightly. Because the error generated by the “Adjusted Radii–Hub” formula changes systematically with variation in web and hub asymmetry, we recommend that investigators use this formula only in studies in which web and hub asymmetry are known to be relatively similar between webs to prevent *a priori* biases when comparing capture areas. The “Ellipse–Hub” formula may be the most efficient formula to use. It has a small overall error and relative independence from changes in web and hub asymmetry. Furthermore, the small number of measurements necessary to use the “Ellipse–Hub” formula not only reduces measurement errors, it may also allow the formula to be used on damaged webs in the field when all of the measurements necessary to use a more parameter rich formula might not be possible (e.g. if the hub of a web is damaged). Finally, all formulae use a circular approximation to calculate the area of the free zone. Using an elliptical approximation such as that used to calculate the total area of the web in the “Ellipse–Hub” formula would further improve estimation of capture areas of orb webs.

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ACROGRAPHINOTUS MITMAJ, A NEW HARVESTMAN SPECIES FROM CENTRAL PERU (OPILIONES, GONYLEPTIDAE, PACHYLINAE)

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ABSTRACT. This paper presents the description of the new species, *Acrographinotus mitmaj* (Opiliones, Gonyleptidae, Pachylinae). It can be easily distinguished from its congeners by: male femur IV long and spiny, devoid of the rows of tubercles and/or apophyses characteristic of other nominal species in the genus; further, *A. mitmaj* new species bears a less developed median apophysis on the 3rd free tergite (larger armature in other species). Penis morphology (especially concerning the ventral process of the stylus) agrees with the generic diagnosis. Known localities of the new species are restricted to the upper Río Cañete valley (Departamento Lima, central Peru).

RESUMEN. Se describe la nueva especie *Acrographinotus mitmaj* (Opiliones, Gonyleptidae, Pachylinae). Ésta puede distinguirse fácilmente de otras especies en el género por el fémur IV del macho, largo y espinoso, sin las hileras de tubérculos y/o apófisis que caracterizan a los otros *Acrographinotus*; asimismo, *A. mitmaj* n. sp. presenta la apófisis mediana del 3er tergito libre menos desarrollada (dicha apófisis es mayor en otras especies). La morfología del pene (en especial del proceso ventral del stylus) concuerda con la diagnosis genérica. Las localidades conocidas de la nueva especie se limitan al valle superior del Río Cañete (Departamento Lima, Perú central).

Keywords: Opiliones, Gonyleptidae, *Acrographinotus*, Perú, Andes

In a previous paper (Acosta 2001) the taxonomic concept of the Andean genus *Acrographinotus* Holmgren 1916 (Opiliones, Gonyleptidae, Pachylinae) was reviewed and updated. Aside from several morphological characters formerly accepted (armature of scutum and ocular mound, number of tarsomeres (Roewer 1929; Soares & Soares 1954)), the penis morphology proved once again to be the best source for generic diagnostic features. Penes in this genus are characterized by the ventral process of stylus, which was described to recall a “round-combed ibis head” (Acosta 2001): distal end dilated, armed with a curved projection, and covered by a membranous expansion.

As already stated (Acosta 2001), the few subsequent references to the type species, *A. erectispina* Roewer 1929, are misidentifications made by its own author (Roewer 1957, 1963). In his 1963 paper, Roewer wrongly identified as *A. erectispina* two lots collected by Wolfgang Weyrauch, one from “Tintin, Río Cañete” in Central-West Peru, the remaining (supposedly) from “Cueva de San

Andrés”, in Departamento Cajamarca, Northern Peru. These specimens represent a still unnamed entity, here described as *Acrographinotus mitmaj*. In one lot there is also a mistake of transcription in Roewer’s handwritten label: specimens that were published from “Cueva de San Andrés” were actually caught in “Yauyos” (as indicated in the original labels by Weyrauch), a locality near Tintin. Yauyos and Tintín (Departamento Lima, Perú) are until now the only known localities of this new species.

The genus *Acrographinotus* is known to exist in a wide range along the Andean region, from northern Peru to northern Argentina (Acosta 2001). Most specimens (both those mentioned in the literature, and new material so far studied by me) were collected in sites situated either in the eastern Andean watershed, inter-Andean valleys, or high-Andean (Puna) biotopes. The only three species hitherto known from the western Andean slopes occur in Departamento Lima, mid-Peru (Roewer 1929, 1956, 1957): *Acrographinotus curvispina* Roewer 1929, *A. ortizi* (Roewer

1957), and *A. mitmaj*. While the penis morphology of the latter undoubtedly conforms to the generic concept, the external appearance diverges from all congeners, as briefly discussed below. At the moment, *Acrographinotus* contains two nominal species from Bolivia (*A. erectispina*, *A. niawpaq* Acosta 2001) and four from Perú (*A. curvispina*, *A. ortizi*, *A. ceratopygus* (Soares & Bauab 1972), *A. mitmaj*); no fewer than nine species still remain to be described (Acosta 2001 and unpubl. data). Specimens studied are deposited in the Senckenberg Museum, Frankfurt (SMF, RII: Collection Roewer II), and in the author's collection, Córdoba, Argentina (LEA).

Acrographinotus mitmaj new species

Figs. 1–12

Acrographinotus erectispina: Roewer 1963:59 (misidentification).

Type series.—Male holotype (SMF 39175—ex SMF RII 13957), 1 male paratype (SMF RII 13957), **PERÚ**: Tintín, Río Cañete, 24 March 1960 (W. Weyrauch). Female allotype, 6 males, 13 females paratypes (SMF RII 13956), 1 male, 1 female paratypes (LEA 000.142), Perú: Yauyos, Río Cañete, 10 January 1960 (W. Weyrauch) (mislabelled “N. Perú: Cueva de San Andrés” by Roewer).

Etymology.—The Quechua noun *mitmaj* (“mitimae” in Spanish) designates any group of subjects—even an entire village—the Inca emperors decided to displace and resettle within the Empire, either for administrative, economic, cultural or military interests. Specimens in one of the vials I studied were mislabelled by Roewer as collected in North Peru (and so published under *A. erectispina*), but were actually captured in Yauyos. The species name is thus an elliptical reference to Roewer's error.

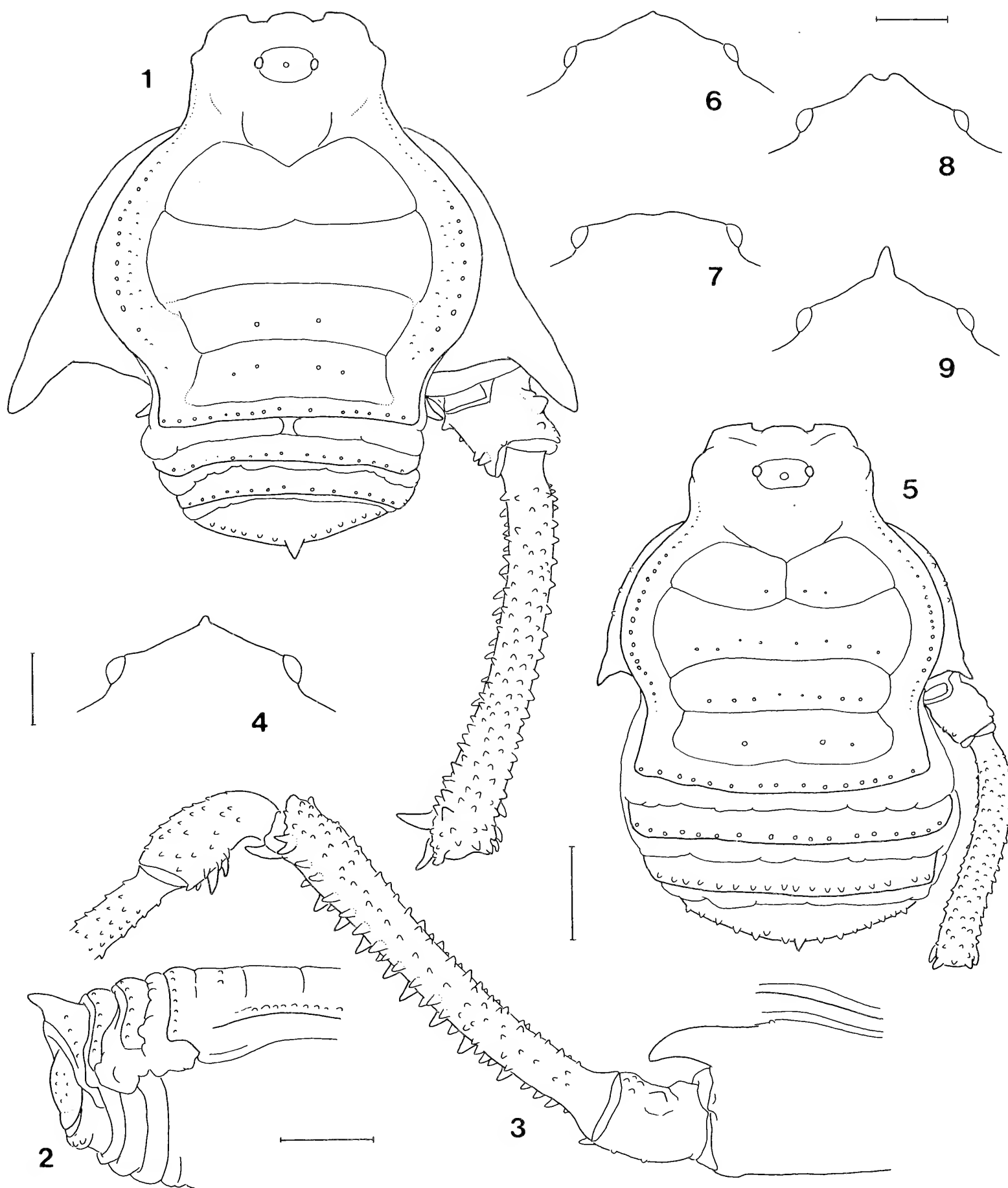
Type locality.—**PERÚ**, *Departamento Lima*, Tintín (3100 m), 12°18'S, 75°49'W.

Diagnosis.—Males of *A. mitmaj* are easily identified by the spiny and rather simple femur and tibia IV (Figs. 1, 3); most congeners have rows of blunt tubercles on the femur, in many species this article is also armed with differently shaped dorsal apophyses (cf. Acosta 2001). While the habitus of the males of *Acrographinotus* is very characteristic, because of the markedly diagonal articulation of trochanter IV, this is much less noticeable in *A. mitmaj* (Fig. 1). Such peculiar external

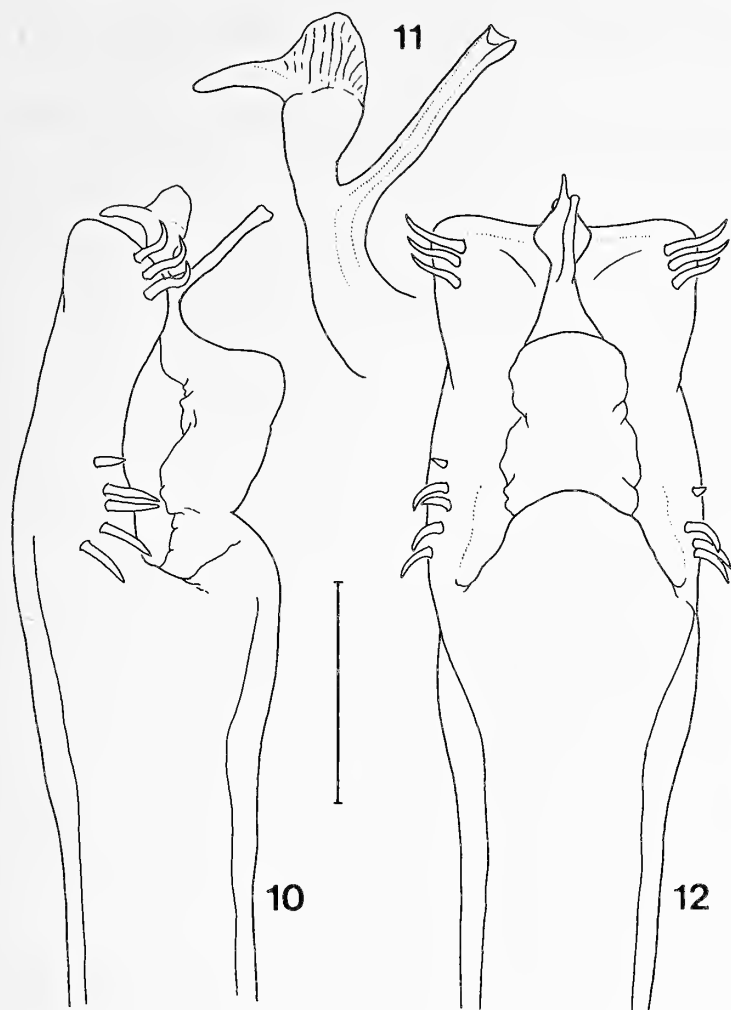
morphology puts the new species in an isolated position in the genus. Like other *Acrographinotus*, males bear a median apophysis on the 3rd free tergite, though comparatively much less developed in *A. mitmaj*. Features such as the number of tarsomeres, and armature of the scutum and the ocular mound agree with those of the genus.

Description.—Measurements of male holotype and female allotype: Table 1. Dorsal scutum length: males 6.76–9.53 mm (\bar{x} = 8.04 mm, n = 9), females 6.41–7.58 mm (\bar{x} = 7.28 mm, n = 15). General color light hazel, the prosoma shows a faint pigmentary reticulation, which extends to the scutum edges and to the ventral side; areas I–V and free tergites lighter; leg IV from coxa to tibia darker and more reddish; chelicera, pedipalps, legs I–III, distal portion of tibia IV, metatarsus and tarsus yellowish.

Male: Ocular mound normally with unpaired armature, varying from completely unarmed to armed with spiniform apophysis; the latter may be blunt or be replaced by double, blunt lobulation (paired!)(see variability below and Figs. 6–9). Scutum unarmed, tegument with matt texture (under higher magnification a delicate granulation is observed). All scutal areas may have very few, inconspicuous, minute granules (generally, area V, free tergites and lateral areas bear one row of granules, while in remaining areas granules are sparse). Free tergite III with short apophysis, normally pointed obliquely upwards (see Variability and Fig. 2), with a row of small acute granules on each side. Dorsal and ventral anal plate with granulous border, ventral one with a pair of paramedian, slightly larger granules. Legs I–III unarmed, granulous. Leg IV: Coxa smooth, prolateral apophysis strong, slightly curved in lateral view; a short, hook-shaped retrolateral apophysis can be seen in ventral view between trochanter IV and the first sternite. Trochanter articulated slightly sideways, with small apophyses: prolateral apophysis uni- or bilobate; proapical edge with slight tubercle or granule group; one or two small acute retroapical apophyses; retroproximal apophysis opposed to retrolateral apophysis of coxa IV; small acute ventroapical apophysis, projecting over the trochanter-femur joint. Femur almost straight, with slight gradual thickening toward distal end; spiny appearance because of longitudinal rows of



Figures 1-9.—*Acrographinotus mitmaj* new species. 1-4. Male holotype. 1. Dorsal scutum, free tergites, coxae IV, right trochanter and femur IV, dorsal view. 2. Lateral view of free tergites, sternites and anal operculum. 3. Right coxa, trochanter, femur and patella IV, lateral view. 4. Ocular mound, posterior view. 5. Female allotype, dorsal scutum, free tergites, coxae IV, right trochanter and femur IV, dorsal view. 6-9. Variations of the ocular mound (paratypes), posterior view (Fig. 7 is a male, the remaining are females). Scale lines = 2 mm in Figs. 1-3, 5, 0.5 mm in Figs. 4, 6-9.



Figures 10–12.—*Acrographinotus mitmaj* new species. Distal end of penis (holotype). 10. Lateral view. 11. Detail of stylus and ventral process. 12. Dorsal view. Scale line = 0.2 mm.

acute equally-sized granules or tiny apophyses (Fig. 1); retroventral row with larger apophyses (Fig. 3); distal end with two ventromedial, hook-like larger apophyses: the subdistal pointed medially, the distal one (united to the former by its base) points posteriorly; proventral row ends in a bifid apophysis (or two apophyses, very close). Patella granulous, with 3–4 large spiniform apophyses and several smaller ventral apophyses. Tibia like femur, spiny and expanded toward distal tip, dorsum with much smaller granules, ventrum with pro- and retroventral rows of acute apophyses, increasing in size to distally (retroventral apophyses much larger). Metatarsus spiny and thick compared to tarsus. Penis (Figs. 10–12): truncus not dilated subterminally, the ventral plate shows the generic pattern of spine-like setae; stylus with characteristic “ibis head-shaped” ventral process, as described for the genus (Acosta 2001).

Female: Color more uniform than male, only pedipalps and legs I–III lighter. Granulation of dorsal scutum as in male, granules of free tergites somewhat taller and more

acute, especially on free tergite III (a median granule is larger, corresponding to the apophysis of male). Coxa IV with conic, prolateral apophysis, and row of low granules under the scutum edge; tiny retrolateral apophysis. Trochanter IV with sparse granules. Femur IV with rows of acute granules; two apical apophyses slightly larger, one ventromedial—pointing downwards—the other ventrolateral (bifid).

Variability.—*Ocular mound* ($n = 24$): Most specimens bear a single, acute apophysis ($n = 13$), either low ($n = 6$, among them the holotype, Fig. 4) or tall ($n = 7$, Fig. 9). Three specimens have a low, blunt mound. A paired condition was observed in 8 individuals, ranging from a pair of very low mounds with a subtle median notch in between (Fig. 7), to more elevated apophyses, blunt and rounded-tipped (Fig. 8). Females have comparatively higher ocular mounds than males.

Apophysis of the 3rd free tergite: Only in four males (holotype included) is this apophysis pointing upwards; in the remaining five it is either curved (the tip points downwards) or horizontal. In the females, the tiny apophysis can be diagonally upwards-pointing ($n = 10$) or horizontal ($n = 5$).

Femur IV length/scutum length ratio (males): Femur IV length (FL) varies allometrically (+) with respect to the scutum length (SL): in males with scutum less than 8 mm, the femur is shorter than the scutum; with scutum length over 8 mm the femur is longer than the scutum. Specimens with extreme values: min. = FL 5.4, SL 6.8; max. = FL 11.7, SL 9.5. Mean ($n = 9$): FL 8.0, SL 8.0. The apical thickening of the femur IV is more evident in smaller specimens.

Number of tarsal segments, leg II: males ($n = 17$) with 8 ($n = 12$) or 9 tarsomeres ($n = 5$), females ($n = 30$) with 7 ($n = 4$), 8 ($n = 25$) or 9 ($n = 1$) tarsal segments.

Distribution.—Only known from two localities in the upper Río Cañete Valley (Mid-Perú, western slopes of the West Andes): the type locality, and Yauyos (3100–3200 m – 12°27'S, 75°54'W), situated less than 20 km away from the former.

DISCUSSION

Roewer (1929, 1963) paid excessive attention to a single diagnostic character (shape of apophysis on 3rd free tergite) to separate his

Table 1.—Measurements (mm) of the holotype male and allotype female of *Acrographinotus mitmaj* new species.

	Holotype male	Allotype female
Total body length (apophysis included)	10.86	10.86
Scutum, length/maximal width	8.10/7.69	7.53/6.46
Prosoma length/width	2.97/3.84	2.77/3.59
Leg I, total length/femur	15.78/4.02	12.60/3.25
Leg II, total length/femur	26.40/6.84	19.25/4.80
Leg III, total length/femur	22.81/6.19	16.77/4.39
Leg IV, total length	36.46	22.71
trochanter	2.20	1.36
femur	9.12	5.35
patella	3.16	2.20
tibia	8.25	4.83
metatarsus	10.51	6.34
tarsus	3.22	2.63
Pedipalp, total length/femur	10.08/2.50	8.71/2.21
Chelicera, total length	3.87	3.38
Ocular mound, width/height	1.32/0.47	1.20/0.41

two species, *A. erectispina* and *A. curvispina*, the former with an upwards pointing apophysis, the latter with a curved, downwards pointing one. This is not only an oversimplification but was also based in an erroneous judgement of the character in *erectispina* (the supposedly erect apophysis is most likely just an artifact of the holotype, caused by the contracted opisthosoma (Acosta 2001)). As previously indicated, the condition of the apophysis varies intraspecifically in *A. mitmaj*, and actually in a few specimens it points upwards. In any case, when comparing the rest of the morphology, so different in most features, Roewer’s misidentifications are at least surprising. Another character that was formerly misunderstood is the armature of the ocular mound. The genus was traditionally characterised as bearing “unpaired armature” (Roewer 1929), while, for example, the genus *Liographinotus* Roewer 1957 (now under synonymy of *Acrographinotus* (Acosta 2001)), was armed with two small tubercles (paired armature). It is now clear that the armature of the ocular mound is a reliable character in species with a tall tuber oculorum (e.g., *A. curvispina*), but is highly variable when the ocular mound is low (as for example, *A. ortizi* and *A. mitmaj*). In the latter, some specimens show a single median tubercle or small apophysis, while other individuals have no armature of any kind; others finally have a slight me-

dian depression instead, giving the elevated laterals of this notch the appearance of paired tubercles (cf. Fig. 8). It is to be noted that such a variable condition was once used to define a monotypic genus (*Liographinotus*).

ACKNOWLEDGMENTS

For the loan of Roewer’s materials I am indebted to Dr. Manfred Grasshoff and Mrs. Ulrike Schreiber (SMF). This research was partially supported by the Argentinian Consejo Nacional de Investigaciones Científicas y Técnicas (P.E.I. 0406/97).

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NEW SPECIES OF EREMOBATIDAE (ARACHNIDA, SOLIFUGAE) FROM NORTH AMERICA

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ABSTRACT. Five new species of Solifugae are described from North America: *Eremobates chihuahensis*, *Eremobates gerbae*, *Hemerotrecha sevilleta*, *Hemerotrecha cornuta*, *Eremochelis oregonensis* as well as the females of *Eremocosta gigasella* (Muma, 1970), and *Eremobates polhemusi* Muma & Brookhart, 1988.

Keywords: Taxonomy, solpugida, camel spiders, sun spiders, wind scorpions

The solifuges of North America are among the best known in the world due to the extensive publications of the late Martin Muma. The last major taxonomic publications dealing with North American solifuges (Muma 1987, 1989; Muma & Brookhart 1988) raised the number of named taxa in U.S.A. and Canada to 175 species in 10 genera, of which four genera belong to the Ammotrechidae (*Ammotrecha* Banks, *Ammotrechella* Roewer, *Ammotrechula* Roewer and *Branchia* Muma) and seven belong to the Eremobatidae (*Eremobates* Banks, *Eremocosta* Roewer, *Eremorhax* Roewer, *Horribates* Muma, *Chanbria* Muma, *Eremochelis* Roewer, *Eremothera* Muma, and *Hemerotrecha* Banks).

Despite this impressive tally, new species are constantly being discovered, and our examination of material from Sevilleta Long Term Ecological Research Site (LTER), Socorro County, New Mexico, along with material collected by the authors and material sent for inspection from various institutions has identified five new eremobatid species and the first females of *Eremobates polhemusi* Muma & Brookhart 1988 which had been described from a single male, and *Eremocosta gigasella* Muma 1970 which had been described from several males collected in Texas and Mexico. Descriptions of these species are presented below.

METHODS

Measurements were made using the methods described by Muma (1951, 1962 & 1970)

and Brookhart & Muma (1981). Microscopic measurements were made at 25x using a Bausch and Lomb Stereozoom 7 binocular microscope. A glass slide was lightly pressed across the structures of smaller specimens in order to impose a level plane of measurement. This was particularly useful in measurements of the propeltidium and the female genital operculum. Gross measurements using a plastic ruler were made to the nearest 0.5 mm. Measurements using the ocular micrometer were made to the nearest 0.1 mm. Drawings were made using a camera lucida mounted to an Olympus S7H binocular microscope. Measurements given in the description are in millimeters. Paratype measurements are given as ranges where appropriate. Ratios listed below were used as described in Muma (1951), Brookhart & Muma (1981), and Muma & Brookhart (1988). Diagrams illustrating the method of measurement can be found in Muma & Brookhart (1988). Additionally we used the ratio of chelicera width to width of fixed finger in those species in which the fondal notch was absent or obscure.

Abbreviations: PT = principal tooth; AT = anterior tooth; MT = medial tooth; IT = intermediate tooth; MST = mesal tooth; PL = propeltidium length; PW = propeltidium width; CL = chelicera length; CW = chelicera width; FFW = fixed finger width; FL = fond length; FW = fond width.

Ratios: A/CP: The sum of the lengths of the palpus, leg I and leg IV divided by the sum of length of the chelicera and propeltidium in-

dicating length of legs in relation to body size. The larger the number, the longer legged is the species. FL/FW indicates whether the chelicera fondal notch is longer or wider. Longer is defined as the anterior to posterior axis and width is defined as the dorsal to ventral axis. FW/FFW diagnoses the size of fondal notch compared to the thickness of fixed finger. CW/FFW is used to indicate whether the fixed chelicera finger is thin or robust in relation to the size of the chelicera. GOL/GOW demonstrates the relative size of the female genital operculum in terms of length and width.

Acronyms used in this paper are as follows: AMNH = American Museum of Natural History, N. Platnick; BYU = Brigham Young University, Richard Bauman; CSU = Colorado State University, Boris Kondratieff; DMNH = Denver Museum of Nature and Science, Paula Cushing; UNM = University of New Mexico, Sandy Brantley and Dick Fagerlund; USU = Utah State University, Wilford Hansen.

Family Eremobatidae Kraepelin 1901

Subfamily Eremobatinae Kraepelin 1901

Genus *Eremobates* Banks 1900

Eremobates gerbae, new species

Figs. 1–7

Material examined.—Male holotype, female allotype, 2 ♂ and 1 ♀ paratype collected from wet pitfall traps at Mack Burn Area, Rincon Mountains, Cochise County, Arizona, USA by Peggy Gerba, 14 August–8 October, 1995 (deposited at DMNH).

Etymology.—This species is named for the collector, Peggy Gerba of Tucson, Arizona.

Diagnosis.—*Eremobates gerbae* is placed in the *E. pallipes* group (Muma 1951) based on the shape of the mesal groove of the male fixed finger, the shape of the dorsal aspect of the male fixed finger, and the shape of the female genital operculum. It appears to be closely related to both *E. durangonus* Roewer 1934 and *E. suspectus* Muma 1951. Males of *E. gerbae* are distinguished from both by the presence of palpal papillae which are absent in *E. durangonus* and *E. suspectus*. Male coloration is much lighter than *E. durangonus*. The male fondal notch of *E. gerbae* is wider than its length while *E. suspectus* is longer than wide. The medial notch of the genital operculum in *E. gerbae* is wide, almost equal to its width, and extends approximately two thirds of the medial opercular length as op-

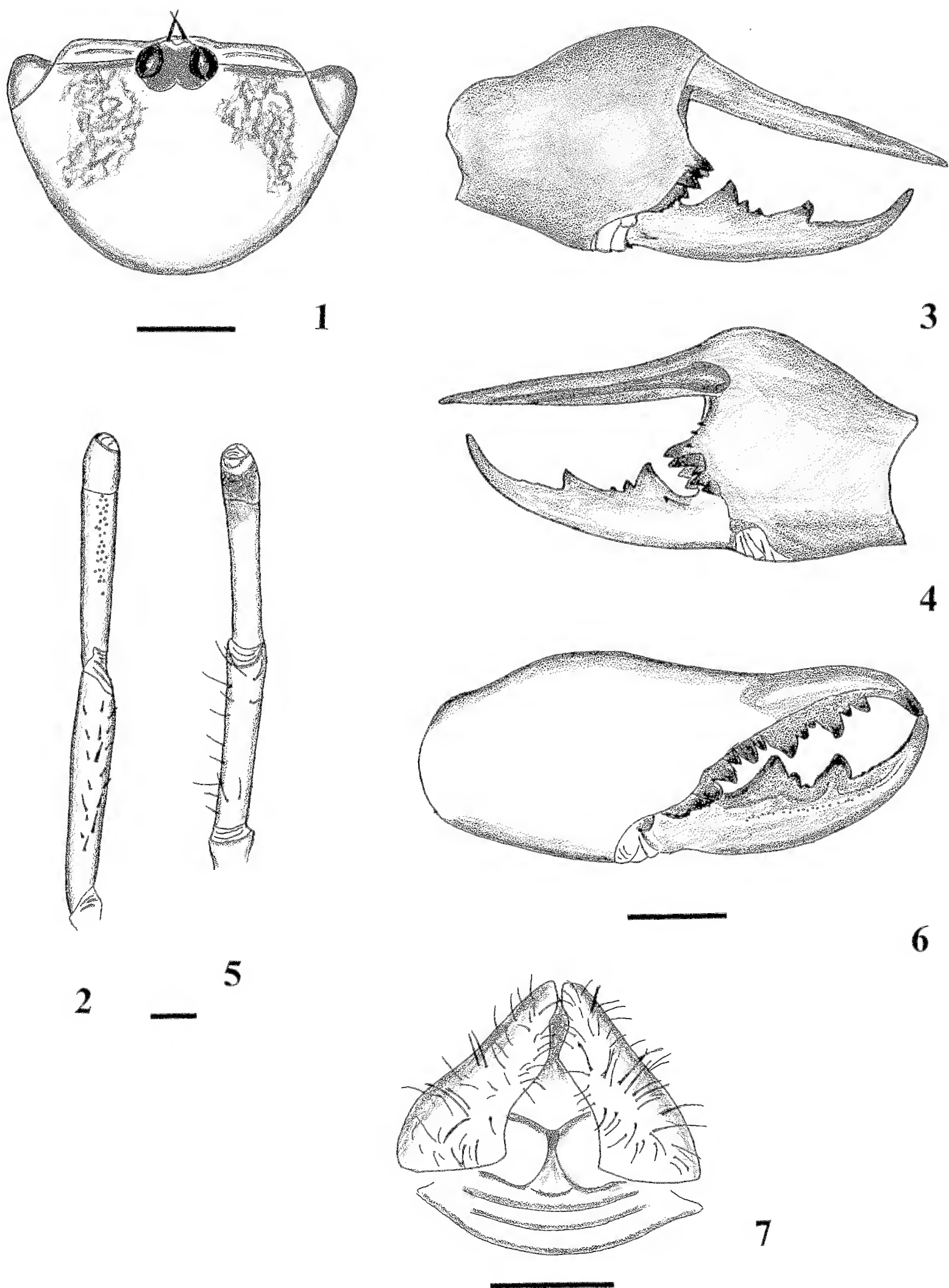
posed to one fifth in *E. durangonus* and one third in *E. suspectus*.

Description.—*Male holotype*: total length 22, chelicera length 5.1, chelicera width 2.3, propeltidium length 2.4, propeltidium width 3.4, palpus length 16, first leg length 11.5, fourth leg length 22. *Ratios*: A/CP 6.8, CL/CW 2.3, FL/FW 0.6, WFF/FW 0.5, CW/WFF, 8.1. *Male paratypes* (2): total length 22.5–25, chelicera length 4.1–5.2, chelicera width 1.7–2.4, propeltidium length 2.1–2.4, propeltidium width 2.7–3.4, palpus length 16–19, first leg 11.4–12, fourth leg 19–23. *Ratios*: A/CP 7.1–7.5, CL/CW 2.0–2.4, FL/FW 0.5–0.7, WFF/FW 0.6–0.7, CW/WFF 6.1–8.6.

Overall color in alcohol dusky yellow. Propeltidium slightly darker than rest of body with brownish-violet blotches anteriorly, eye tubercle dark, abdominal tergites dusky. Palpal tarsi, metatarsi, and anterior edges of propeltidium tinged a faint brownish violet (Figs. 1 & 2), malleoli white. Chelicerae without markings. Fixed finger straight, smooth ventrally, typical of *pallipes* group with a well defined, narrow mesoventral groove extending from tip of chelicera ending in a cup basally beneath the flagellum complex. Movable chelicera finger with larger PT and smaller AT, two distinct IT between PT and AT, the posterior larger and located at the notch of PT and dorsal edge of FF. MST intermediate in size. Fondal notch wider than long with 2–3 small denticles visible mesally. Relative size of fondal teeth graded I, III, II, IV ectally and mesally (Figs. 3 & 4). Flagellum complex typical of *Eremobates* group with apical plumose bristle large, distinct, occupying approximately 75% of mesoventral groove. Palpus with 35–48 small, white, rounded papillae on palpal metatarsus (Fig. 2). No ctenidia on first post-spiracular sternite.

Female allotype: total length 18, chelicera length 5.1, chelicera width 2.1, propeltidium length 3.0, propeltidium width 3.8, palpus length 17, first leg length 12, fourth leg length 18. *Ratios*: A/CP 5.8, GOL/GOW 0.6. *Female paratype*: total length 20, chelicera length 5.2, chelicera width 2.2, propeltidium length 2.9, propeltidium width 3.6, palpus 19, first leg length 12, fourth leg length 16. *Ratios*: A/CP 5.8, GOL/GOW 0.9.

Coloration in alcohol as in the males. Palpus lightly tinged brownish-violet on tarsus and distal end of metatarsus, without palpal



Figures 1-7.—*Eremobates gerbae* new species. 1-4. male holotype. 1. Male propeltidium, dorsal view; 2. Male right palpus, mesoventral view; 3. Male right chelicera, ectal view; 4. Male right chelicera, mesal view. 5-7. female allotype. 5. Female right palpus, mesoventral view; 6. Female right chelicera, ectal view; 7. Female genital operculum, ventral view. Scale bar = 1 mm.

papillae or ctenidia (Fig. 5). Fixed chelicera finger with PT and MT large, AT smaller. Two small but defined IT between PT and MT, one IT between MT and AT. Movable chelicera finger with large PT, a slightly smaller AT, 2 distinct IT and a visible MST (Fig. 6). Genital operculum distinctive with two separated, raised sclerotized plates, posterior edges straight, interior margin U-shaped for three fourths of its length, anterior arms undulate at the margins (Fig. 7).

Remarks.—Males of *Eremobates gerbae* go to key couplet seven in Brookhart and Muma (1981) which separates *E. durangonus* and *E. suspectus*. The type locality lies somewhat between that of *E. durangonus* which apparently reaches its northern limits in SW New Mexico and *E. suspectus* which is endemic to the White River Basin of Arizona (Brookhart & Muma 1981). *E. gerbae* is known only from type locality.

Eremobates chihuaensis new species
Figs. 8–12

Material examined.—Male holotype and male paratype from 22 miles SE of Chihuahua, Mexico, 25 August 1980 collected by J. B. Karren from the USU collection (both deposited at DMNH).

Etymology.—The specific name is an abbreviation of the type locality.

Diagnosis.—*Eremobates chihuaensis* is placed in the *Eremobates pallipes* group (Muma 1951) based on the shape and position of the mesoventral groove of the male fixed finger and the unmodified dorsal aspect of the fixed finger of the male chelicera. The relatively large posterior tooth located on the PT of the male MF as well as the narrow mesoventral groove distinguishes it from other species of the group. It goes to couplet two in Brookhart & Muma (1981).

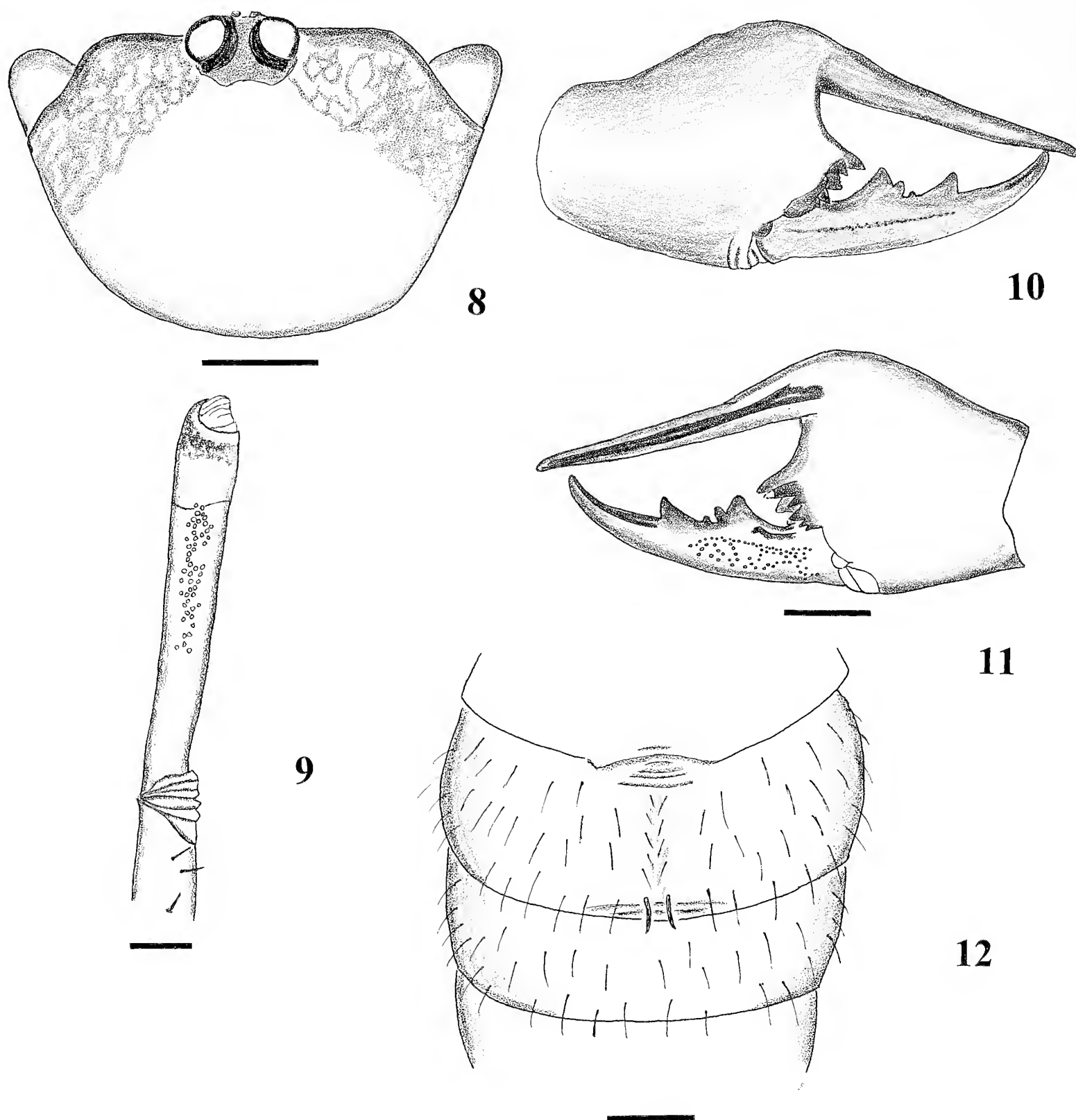
Description.—*Male holotype*: total length 20, chelicera length 6.0, chelicera width 2.8, propeltidium length 3.2, propeltidium width 4.2, palpus length 20, first leg length 15, fourth leg length 20. *Ratios*: A/CP 6.0, CL/CW 2.1, FL/FW 1.7, WFF/FFW 0.83, CW/WFF 4.7. *Male paratype*: total length 23, chelicera length 5.4, chelicera width 2.3, propeltidium length 2.2, propeltidium width 3.7, palpus length 19, first leg length 15, fourth leg length 23. *Ratios*: A/CP 7.5, CL/CW 2.3, FL/FW 1.0, WFF/FFW 0.83, CW/WFF 3.6.

Overall color in alcohol dusky yellow, anterior fringes of the propeltidium blotched brownish-violet; abdominal segments darker both ventrally and dorsally. Palpus tinged with blotched brownish-violet markings at the apical end of tarsus (Figs. 8 & 9). Malleoli white. Chelicera typical of members of *pallipes* group with a deep, thin mesoventral groove running from chelicera tip to under origins of flagella complex, widening slightly posteriorly. Fixed finger narrow, smooth, without denticles. Movable finger with large PT, AT smaller, two IT with the posterior larger and on the PT, MST visible but small. Fondal notch V shaped, longer than wide. Fondal teeth graded I, III, II, IV ectally and mesally (Figs. 10 & 11). Flagella complex typical of *pallipes* group with large apical plumose bristle occupying 90% of mesoventral groove. Palpus with 50–59 small, white papillae on dorsomesal area of palpal metatarsus, entire palpus with numerous short cylindrical setae interspersed with thin, elongated setae. Two short ctenidia on ventral, fourth abdominal segment, extending less than half the length of the succeeding segment (Fig. 12). Females are unknown.

Remarks.—Muma (1987) listed four members of the *pallipes* group from Mexico, *E. dinamita* (Roewer 1934), *E. durangonus* (Roewer 1934), both from Durango, Mexico, *E. putnami* (Banks 1898) from Baja California, and *E. formicarius* (C. L. Koch 1842) from Puebla, Mexico. Brookhart & Muma (1981) also postulated that *E. woodruffi* Brookhart & Muma 1981 was at the northern end of its range in the Big Bend region of Texas because of immatures resembling this species found 3 miles south of Renosa, Mexico in the state of Tamaulipas. Only *E. woodruffi* occupies an area that might be sympatric with *E. chihuaensis*. *E. woodruffi* differs in coloration and male cheliceral profile from *E. chihuaensis*. Females are unknown for both of the previous two species. The relationship of *E. chihuaensis* to each of these species cannot be clarified until more specimens are collected from Mexico.

Eremobates polhemusi Muma & Brookhart
1988
Figs. 13–16

Eremobates polhemusi Muma & Brookhart, 1988:
18–19, figs. 50–52.



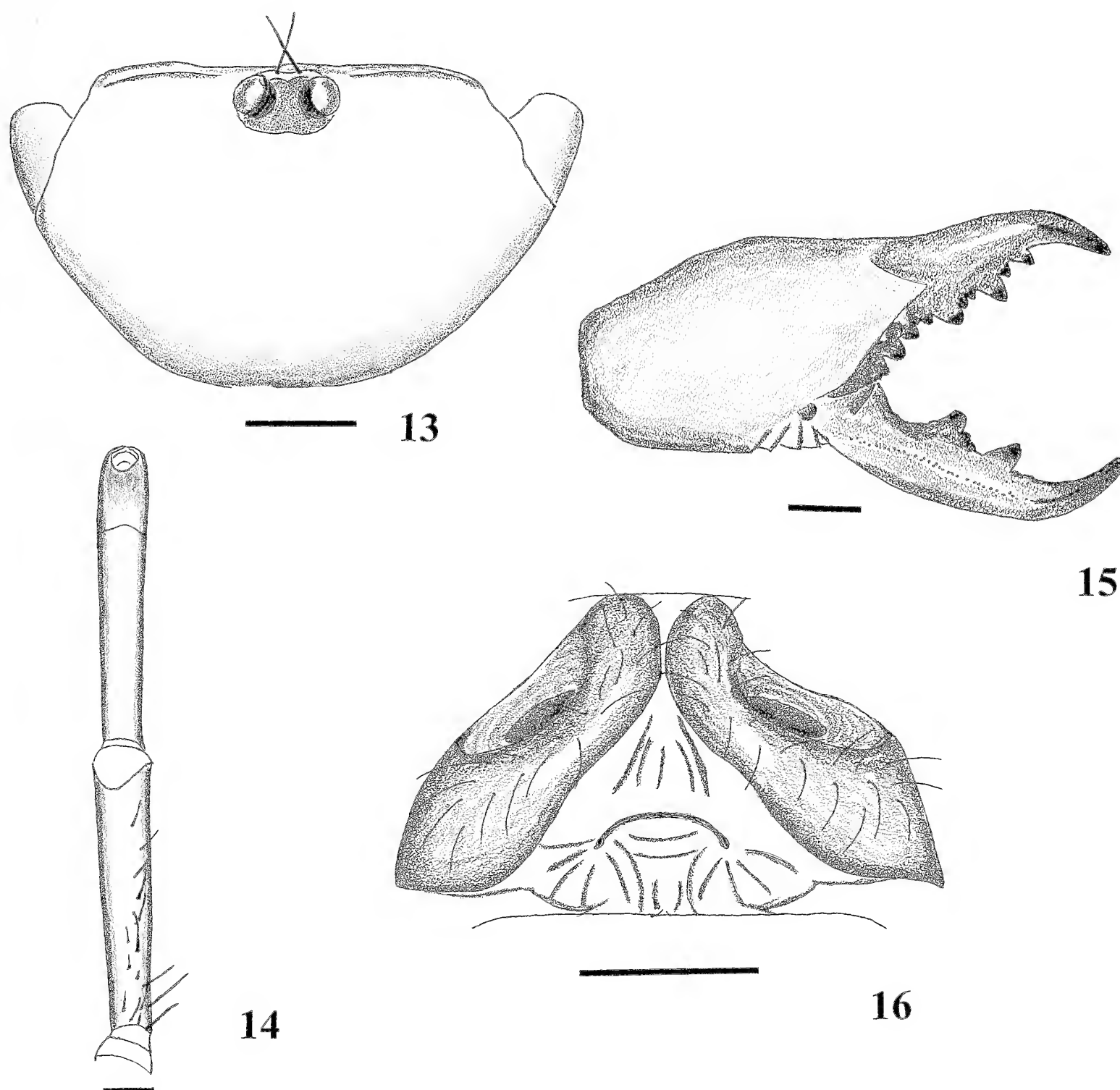
Figures 8–12.—*Eremobates chihuaensis* new species. 8–12, male holotype. 8. Male propeltidium, dorsal view; 9. Male right palpus, mesoventral view; 10. Male right chelicera, ectal view; 11. Male right chelicera, mesal view; 12. Male fourth abdominal segment showing ctenidia, ventral view. Scale bar = 1 mm.

Material examined.—UNITED STATES: **Utah:** *San Juan County:* 3♂, 3♀, 4 miles N. of Bluff, collected by Jack and Irene Brookhart in wet can traps set 27 May 2000 and collected 26 August 2000 (deposited at DMNH). No female allotype designated for this species in original description (Muma & Brookhart 1988).

Description.—*Female:* total length 26, chelicera length 7.2, chelicera width 2.9, propeltidium length 2.9, propeltidium width 5.1,

palpal length 15, first leg length 14, fourth leg length 23. *Ratios:* A/CP 5.1, GOL/GOW 0.5.

Color in alcohol straw yellow to creamy including the propeltidium (Fig. 13); abdomen slightly darker ventrally and dorsally; palpus and legs straw yellow to dusky yellow. Malleoli white. Palpus covered with numerous cylindrical bristles giving a dusky brown coloration to the apical tip of the tarsus (Fig. 14). Chelicera fixed finger with large PT and MT;

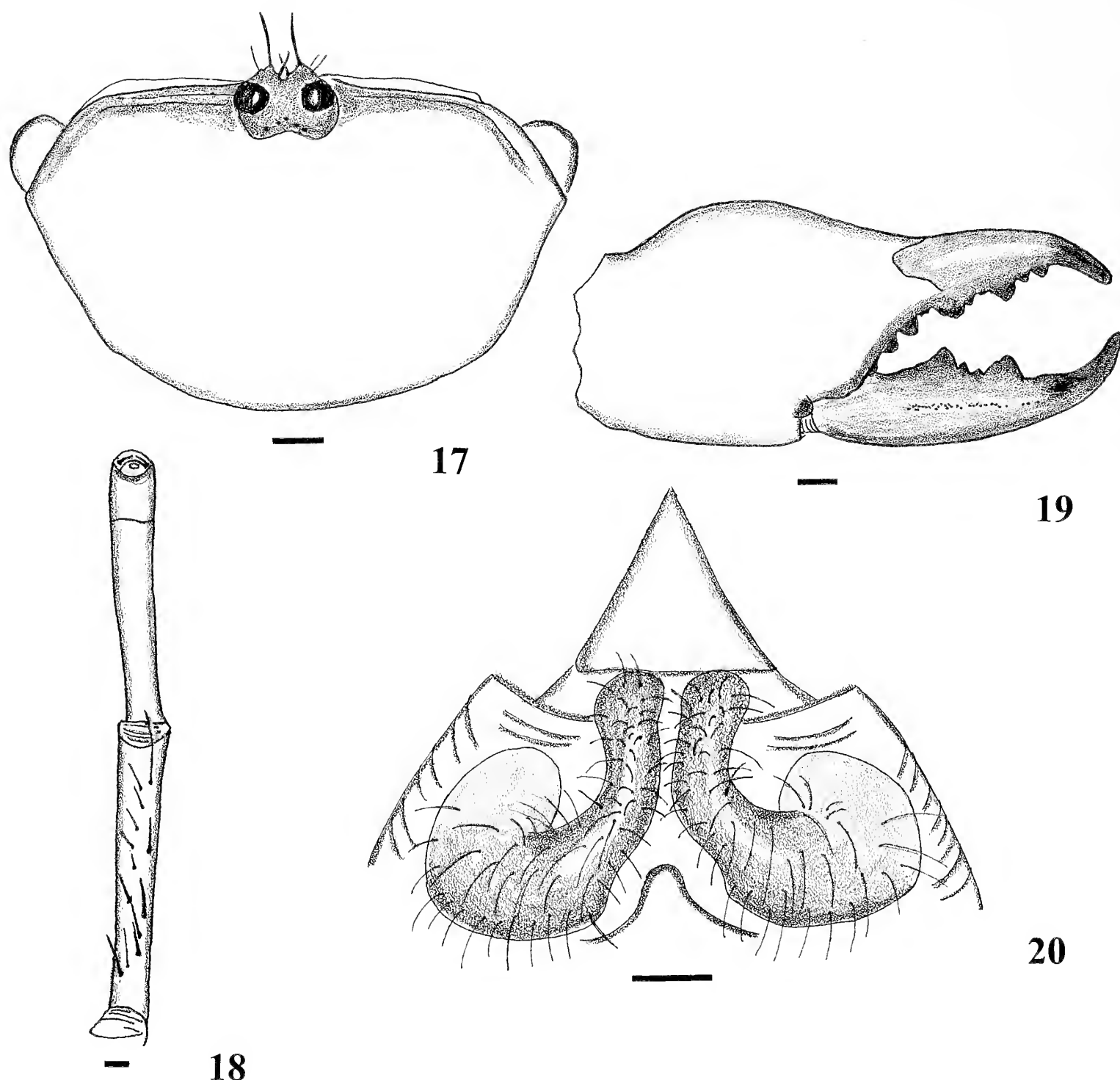


Figures 13–16.—*Eremobates polhemusi* female. 13. Female propeltidium, dorsal view; 14. Female right palpus, mesoventral view; 15. Female right chelicera, ectal view; 16. Female genital operculum, ventral view. Scale bar = 1 mm.

AT half the size of PT, single, small IT between AT and MT, two small IT between MT and PT, MF with large PT and AT, 2 IT between PT and AT, the posterior situated in the notch of the PT. Fonda teeth graded III, II, I, IV ectally and III, I, II, IV mesally, mesal tooth not visible (Fig. 15). No palpal papillae. No ctenidia. Genital operculum typical of *palpisetulosus* group with two separate raised plates, arms slightly enlarged anteriorly and expanded dorsally. Posterior edges flattened and ending in a point on the exterior surface.

Exterior edges curved around a deep opercular pit (Fig. 16).

Remarks.—Muma & Brookhart (1988) identified a single male of *Eremobates polhemusi* from Giddings Trading Post, San Juan County, Utah in their revision of the *Eremobates palpisetulosus* group. The new specimens listed here were from a nearby desert grassland locality. Two other pitfall sites, one in the desert shrub 9 miles north of Bluff, and the other in a piñon-juniper community 14 miles north of Bluff, contained no speci-



Figures 17–20.—*Eremocosta gigasella* female. 17. Female propeltidium, dorsal view; 18. Female right palp, mesoventral view; 19. Female chelicera, ectal view; 20. Female genital operculum, ventral view. Scale bar = 1 mm.

mens of *E. polhemusi* during the same time span.

Genus *Eremocosta* Roewer 1934

Eremocosta gigasella (Muma)

Figs. 17–20

Eremorhax gigas (Roewer): Muma, 1951: 48, figs 32–33 (misidentification).

Eremorhax gigasellus Muma, 1970: 8.

Eremopus gigasellus (Muma): Muma & Muma, 1988: 11.

Eremocosta gigasella (Muma): Harvey, 2001: in press.

Material examined.—UNITED STATES: New

Mexico: Socorro County: 1 ♀, collected in wet can trap, 26 July 1993, Site 222 during survey of Sevilleta LTER (deposited at DMNH).

Diagnosis.—*Eremocosta gigasella* females differ from the related *Eremocosta gigas* (Roewer), a Sonoran species (Muma 1951, 1970) by the position of the IT on the fixed finger which are separated from the PT on *Eremocosta gigasellus* and are located on the PT of *Eremocosta gigas* and by the relative size of the fonal teeth which are graded I, III, II, IV in other members of *Eremocosta* but are graded II, III, I, IV in *E. gigasella*.

Description.—*Female*: total length 26, chelicera length 14.1, chelicera width 6.4, propeltidium length 6.5, propeltidium width 11.0, palpal length 15, first leg length 11.5, fourth leg length 19. *Ratios*: A/CP 2.2, GOL/GOW 0.6.

Coloration of specimen in alcohol straw colored with darker abdominal tergites. Anterior margin of propeltidium dusky (Fig. 17). Malleoli white. Palpi straw colored, with dusky tarsi and apical region of metatarsi (Fig. 18). Dentition of chelicera similar to *Eremocosta striata* (Muma, 1951). Fixed finger with large PT and MT and smaller AT. Two IT between PT and MT and one IT between MT and AT. Movable finger with large PT and AT. Two IT located just anterior to PT. Mesal tooth present. Fondal teeth graded II, III, I, IV ectally and mesally (Fig. 19). Genital operculum as in *E. striata*, (Muma 1951, fig. 31, p. 46), with long raised arms ending posteriorly in a flared flattened inverted funnel like structure. Interior margins undulate. Exterior margins tightly recurved. Posterior margin flattened (Fig. 20).

Remarks.—Muma (1970) renamed some specimens as *Eremorhax gigasellus* that he had previously called *E. gigas* (Roewer 1934), based upon examination of the holotype of *E. gigas*. He designated a male holotype from Boquillas, Texas deposited in AMNH (Muma 1970), and later (Muma 1976) indicated that this species is known only from several males in Texas. A male *Eremocosta gigasella* was also found at the Sevilleta LTER (Brookhart and Brantley 2001). We were unable to find the male from Brewster County, Texas (Muma 1951) which probably represents a specimen of *E. gigasella*. Vázquez (1981) recorded this species from Coahuila and southern Veracruz, Mexico. A female from Chihuahua, Mexico (BYU) also fits this new description. Distribution: Texas, New Mexico, Mexico.

Subfamily Therobatinae Muma 1951

Genus *Hemerotrecha* Banks 1903

Hemerotrecha cornuta new species

Figs. 21–29

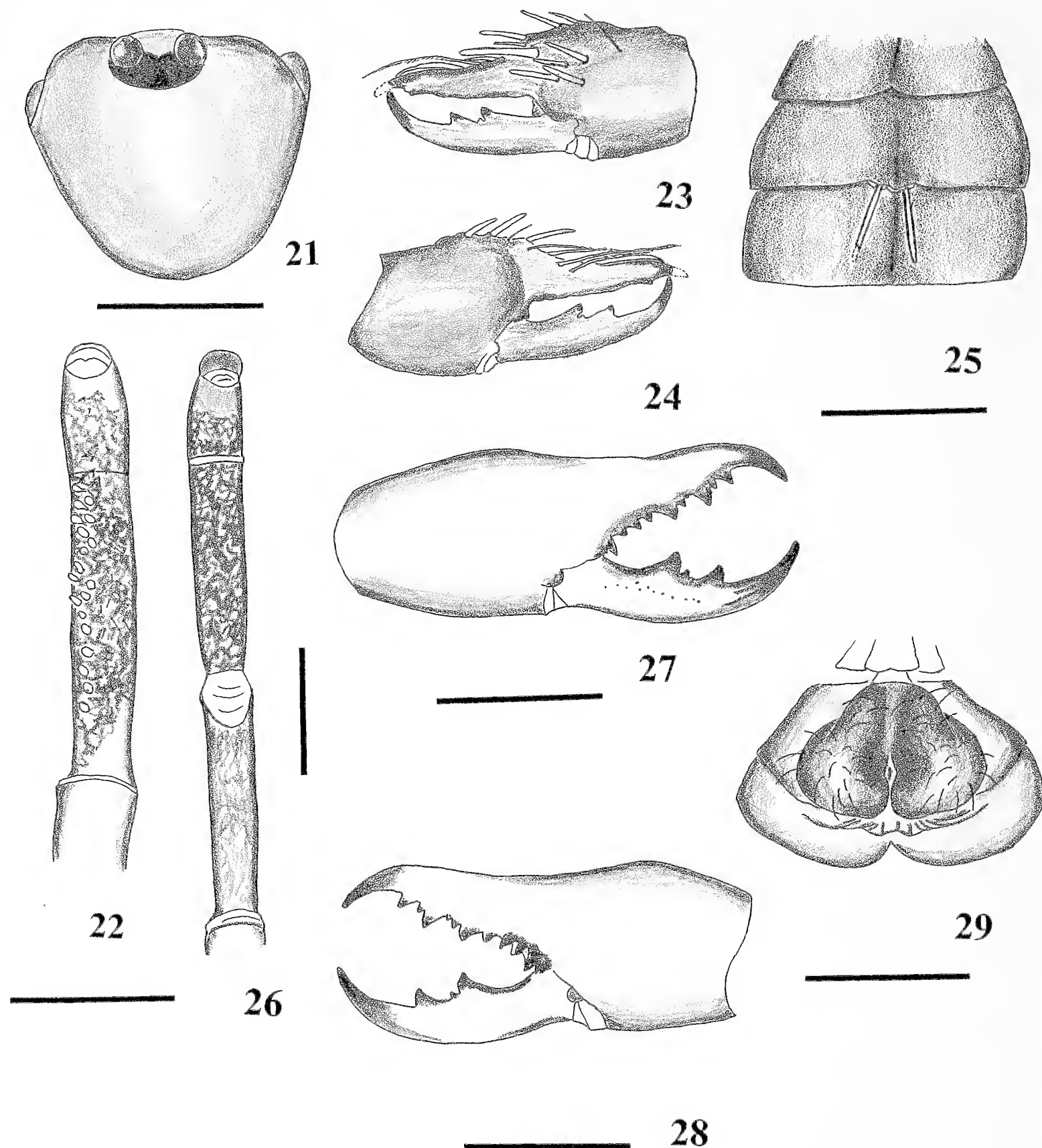
Material examined.—Male holotype, female allotype, 5 ♂ paratypes, and 3 ♀ paratypes collected in wet pitfall traps placed near a gravel wash 6 miles N. of Boone, Colorado, USA, 20 May – 20 June 1976 by Jack Brookhart (deposited at DMNH).

Etymology.—From the latin *cornu* (horn) a description referring to the large horn-like setae on the dorsal surface of the male chelicera.

Diagnosis.—This species is placed in the *Hemerotrecha branchi* group (Muma 1951) based on the structure of the male flagellum complex and the male chelicer profile which has modified but identifiable teeth on the male fixed finger. Females have the characteristic pear-shaped, raised operculum with a longitudinal rather than transverse genital opening. It appears most closely related to *H. sevilleta*, new species, *H. marathoni* Muma 1962 and *H. milsteadi* Muma 1962 known from Texas (Muma 1962, 1970). It is easily identified by the tiny denticles of the male fixed finger, lack of fondal teeth, slightly flatter, wider, shorter ctenidia, and truncated, notched posterior edge of female genital operculum.

Description.—*Male holotype*: total length 8, chelicera length 2.0, chelicera width 0.87, propeltidium length 1.5, propeltidium width 1.8, palpal length 7, first leg length 5.5, fourth leg length 10. *Ratios*: A/CP 6.4, CL/CW 2.3, CW/WFF 4.7. *Male paratypes* (5) – total length 8–12, chelicera length 2.0–2.27, chelicera width 0.8–1.2, propeltidium length 0.6–1.1, propeltidium width 0.8–1.2, palpal length 7–8, first leg length 5.5–6, fourth leg length 9–11. *Ratios*: A/CP 6.3–7.7, CL/1.7–3.3, CW/WFF 3–4.7. Because there was no fond, the ratios FL/FW and WFF/FW were not calculated.

Color in alcohol dusky yellow except for dusky amber markings on tarsus, metatarsus, and tibia of palpus and anterior edges of propeltidium (Figs. 21 & 22). Propeltidium slightly darker than the rest of body, eye tubercle dark, chelicerae without markings, abdominal tergites dusky. Malleoli white. Fixed finger undulate with a small denticle near apical end. Mesal groove obscure. Movable finger with small PT and slightly larger AT. A small IT anterior to PT and separated by a small notch below PT. No fond visible ectally, fond greatly reduced mesally with two tiny teeth. Flagellum complex typical of *branchi* group with flattened striate setae dorsally, apical plumose bristles distinct except the apical bristle which is strongly hooked and blunt tipped, ventral bristles also strongly plumose. Several horn-like setae on the dorsal aspect of the chelicera (Figs. 23 & 24). Palpus with 19–30 large, white, clavate papillae on palpal



Figures 21–29.—*Hemerotrecha cornuta* new species. 21–25, male holotype. 21. Male propeltidium; 22. Male right palpus, mesoventral view; 23. Male left chelicera, ectal view; 24. Male left chelicera, mesal view; 25. Male fourth abdominal segment showing ctenidia, ventral view. 26–29, female allotype. 26. Female right palpus, mesoventral view; 27. Female right chelicera, ectal view; 28. Female right chelicera, mesal view; 29. Female genital operculum, ventral view. Scale bar = 1 mm.

metatarsus (Fig. 22) and several small pointed setae on palpal tarsus and metatarsus. First post-spiracular sternite with two, thin, flat ctenidia extending over less than three-fourths the length of the succeeding tergite (Fig. 25).

Female allotype: total length 10, operculum

length 2.8, operculum width 0.9, propeltidium length 1.2, propeltidium width 1.8, palpal length 7, first leg length 4, fourth leg length 9.5. *Ratios*: A/CP 5.2, GOL/GOW 0.7. *Female paratypes*, (4) total length 10–12, operculum length 2.3–2.9, operculum width 0.8–

1.8, propeltidium length 1.5–2.3, propeltidium width 1.7–2.3, palpal length 6–7, first leg length 4.5–5, fourth leg length 9.5–10.5. *Ratios*: A/CP 4.9–5.3, GOL/GOW 0.6–0.7. Color in alcohol the same as the males. Operculum fixed finger with AT, IT and PT, two smaller teeth separate the PT and MT, a single IT separates the MT and AT. Movable finger with large PT and AT and a smaller IT separated from the PT. Fondal teeth I, II, III equal in size with IV somewhat smaller ectally and mesally (Figs. 27 & 28). No papillae and no spine-like setae on the palpus (Fig. 26). Genital operculum typical of the *branchi* group with two joined, raised, rounded, pear-shaped plates surrounding the genital opening. These plates are expanded laterally at the posterior edges, with a slight notch on the truncated posterior margin (Fig. 29).

Remarks.—The entire type series was collected in wet pit fall traps placed in a gravel wash populated with widely spaced salt bush, *Atriplex canescens*. Brookhart (1972) collected in this area but did not record this species in Colorado, probably because he used dry pit fall traps. Brookhart has also collected this species in wet can traps near Peyton Road, El Paso County, Colorado. Brookhart (1972) recorded another member of the *branchi* group, *H. minima* Muma 1951 from Colorado. Muma (1989) suggests that the entire group may need revision.

Hemerotrecha sevilleta new species
Figs. 30–38

Material examined.—Male holotype, female allotype, 4 ♂ paratypes, and 3 ♀ paratypes collected 29 July 1991 at the Sevilleta National Wildlife Reserve, Socorro County, New Mexico, USA, in wet can traps that are part of the Sevilleta LTER, Wild Fire experimental area (deposited at DMNH).

Etymology.—Named for the Sevilleta LTER collection area and to be treated as a noun in apposition.

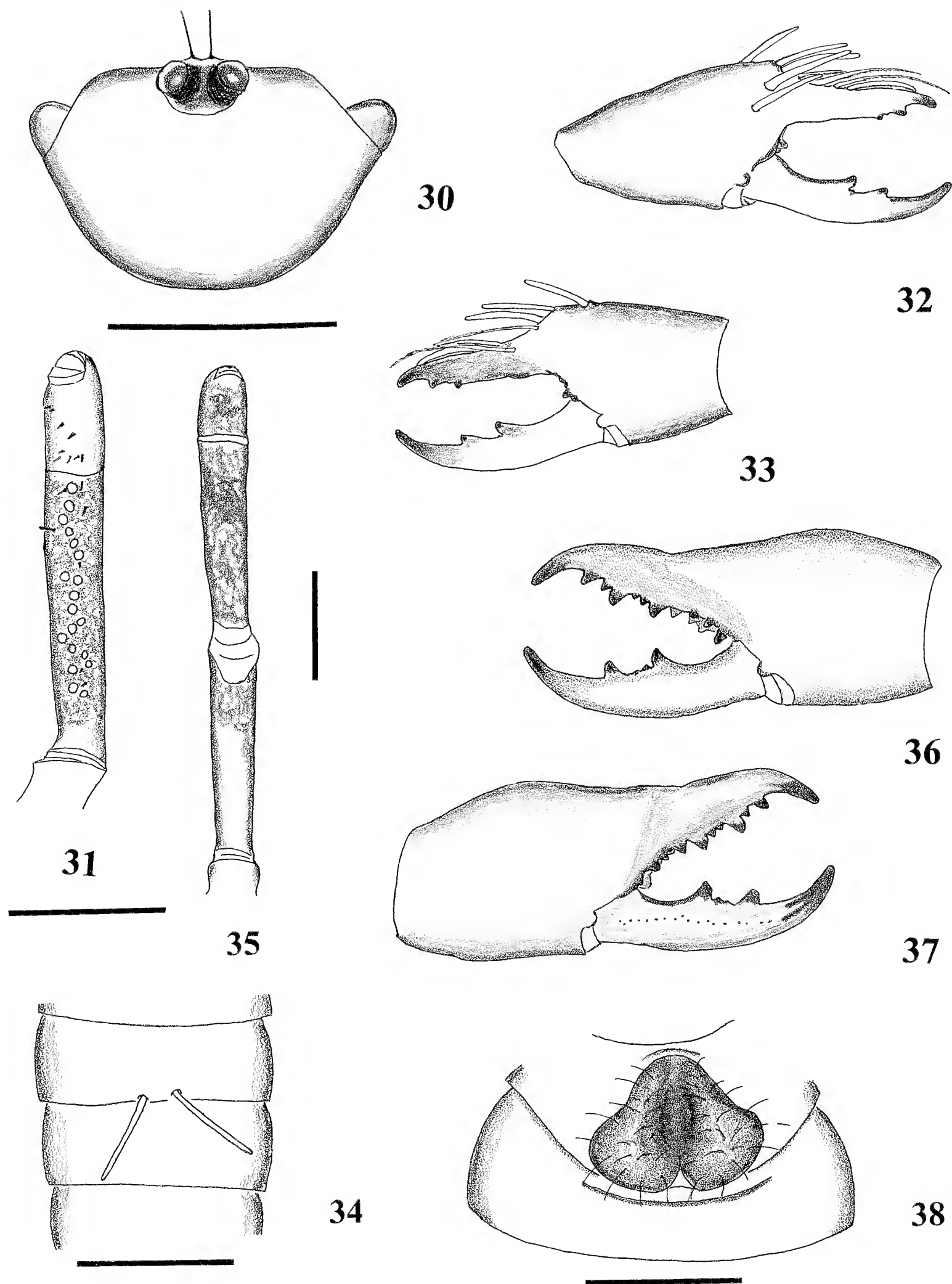
Diagnosis.—This species is placed in the *Hemerotrecha branchi* group (Muma 1951) based on the structure of the male flagellum complex and the male operculum profile which has modified but identifiable teeth. It can be separated from *H. cornuta* by the size and length of ctenidia, dentition of the male fixed finger, visible fondal tooth, and posteriorly rounded shape of female genital operculum. It appears more closely related to *H. mil-*

steadi but can be separated by examining the shape and dentition of the fondal notch.

Description.—*Male holotype*: total length 9, chelicera length 2.5, chelicera width 1.8, propeltidium length 1.1, propeltidium width 1.6, palpal length 7.5, first leg length 6, fourth leg length 10. *Ratios*: A/CP 6.7, CL/CW 3.1, CW/WFF 2.5. *Male paratypes*: (5) total length 8–10, chelicera length 2.1–2.5, chelicera width 1.2–2, propeltidium length 1.3–1.5, propeltidium width 1.3–2.0, palpal length 7.5–8, first leg length 5–6.5, fourth leg length 8–11. *Ratios*: A/CP 5.8–7.3, CL/CW 2.5/2.8, CW/WFF 2.5–3.7. Because there was no visible fond the ratios FL/FW and WFF/FW were not calculated.

Color in alcohol dusky yellow except for dusky markings on tarsus, metatarsus, tibia, and apical 1/3 of femur of palpus and anterior edges of propeltidium (Figs. 30 & 31). Chelicera without markings. Propeltidium slightly darker than rest of body, eye tubercle dark, abdominal tergites dusky. Malleoli white. Fixed finger with two distinct, small, tightly spaced denticles. Movable finger with approximately equal sized PT and AT, tiny IT below notch of PT. Fondal notch obscure ectally and mesally. One, tiny fondal tooth visible ectally, one distinct and one tiny tooth on the fond mesally. Mesal groove not visible. Flagellum complex typical of *branchi* group with flattened striate setae dorsally, apical plumose bristles distinctly plumose except the apical bristle which is strongly hooked and blunt tipped. Ventral bristles strongly plumose. Dorsal surface of chelicerae with several horn-like setae (Figs. 32 & 33). Palpus with 13–25 large white, clavate papillae on palpal metatarsus, palpal tarsus and metatarsus with several small pointed setae (Fig. 31). First post-spiracular sternite with two thin, flat ctenidia extending to or over the margin of the succeeding sternite (Fig. 34).

Female allotype: total length 8.5, chelicera length 2.7, chelicera width 1.1, propeltidium length 1.3, propeltidium width 1.7, palpal length 7, first leg length 5, fourth leg length 8. *Ratios*: A/CP 5.0, GOL/GOW 0.7. *Female paratypes*: (3) total length 8.5–11, chelicera length 2.5–3.3, chelicera width 0.9–1.2, propeltidium length 0.8–1.3, propeltidium width 1.1–2.1, palpal length 6.5–7, first leg length 4–6, fourth leg length 7–11. *Ratios*: A/CP 4.4, GOL/GOW 0.6/0.7. Color in alcohol the same



Figures 30–38.—*Hemerotrecha sevilleta* new species. 30–34. male holotype. 30. Male propeltidium, dorsal view; 31. Male right palpus, mesoventral view; 32. Male right chelicera, ectal view; 33. Male right chelicera, mesal view; 34. Male fourth abdominal segment showing ctenidia, ventral view. 35–39. female allotype. 35. Female right palpus, mesoventral view; 36. Female right chelicera, mesal view; 37. Female right chelicera, ectal view; 38. Female genital operculum, ventral view. Scale bar = 1 mm.

as the males except for a dusky palpal tarsus (Fig. 35). Operculum fixed finger with PT, MT, and AT, two smaller IT separate the PT and MT, a single IT separates the MT and AT. Movable finger with PT and AT and two tiny IT. Fondal teeth graded I, III, II, IV ectally and mesally (Figs. 36 & 37). No papillae and no spine-like setae on the palpus. Genital operculum typical of the *branchi* group with two rounded, pear-shaped, raised plates, apparently connected anteriorly, surrounding transverse genital opening. Posterior edges rounded without a notch. It resembles both *H. marathoni* and *H. cornuta*, new species (Fig. 38). It differs from *H. cornuta* in the shape of the posterior edge of the genital operculum but cannot be separated from *H. marathoni* in the female.

Remarks.—*Hemerotrecha sevilleta* was collected in four of the six study areas in the Sevilleta LTER Project, Socorro County, New Mexico. It was most commonly found in the site called Goat Draw which was a mixed piñon-juniper community. It was also found in three other LTER study areas: Five Points Larrea, Rio Salada Larrea, and a mixed piñon-juniper/scrub oak site called 222. The first two sites are dominated by creosote bush, *Larrea tridentata*. It was not collected in the two dry grassland study sites (Brookhart & Brantley 2001).

Hemerotrecha sevilleta, *H. milsteadi*, *H. marathoni* and *H. macra* Muma 1962 are all found in areas considered to be part of the northern Chihuahua Desert or the adjacent arid grasslands. Whether they are all variants of the same species or sympatric in this area awaits further investigation.

Genus *Eremochelis* Roewer 1934

Eremochelis oregonensis new species

Figs. 39–43

Material examined.—Male holotype, collected by Opler & Buckman, Valley Falls, Lake County, Oregon, USA, 26 May 1999 (deposited in DMNH).

Etymology.—The specific name is a noun in apposition from the state in which it was collected.

Diagnosis.—*Eremochelis oregonensis* is placed in the *Eremochelis branchi* group (Muma 1951) based on the form of flagella complex which has a flattened apical striate setae and a slightly undulate FF. It keys to

couplet three in Muma (1987). Females unknown.

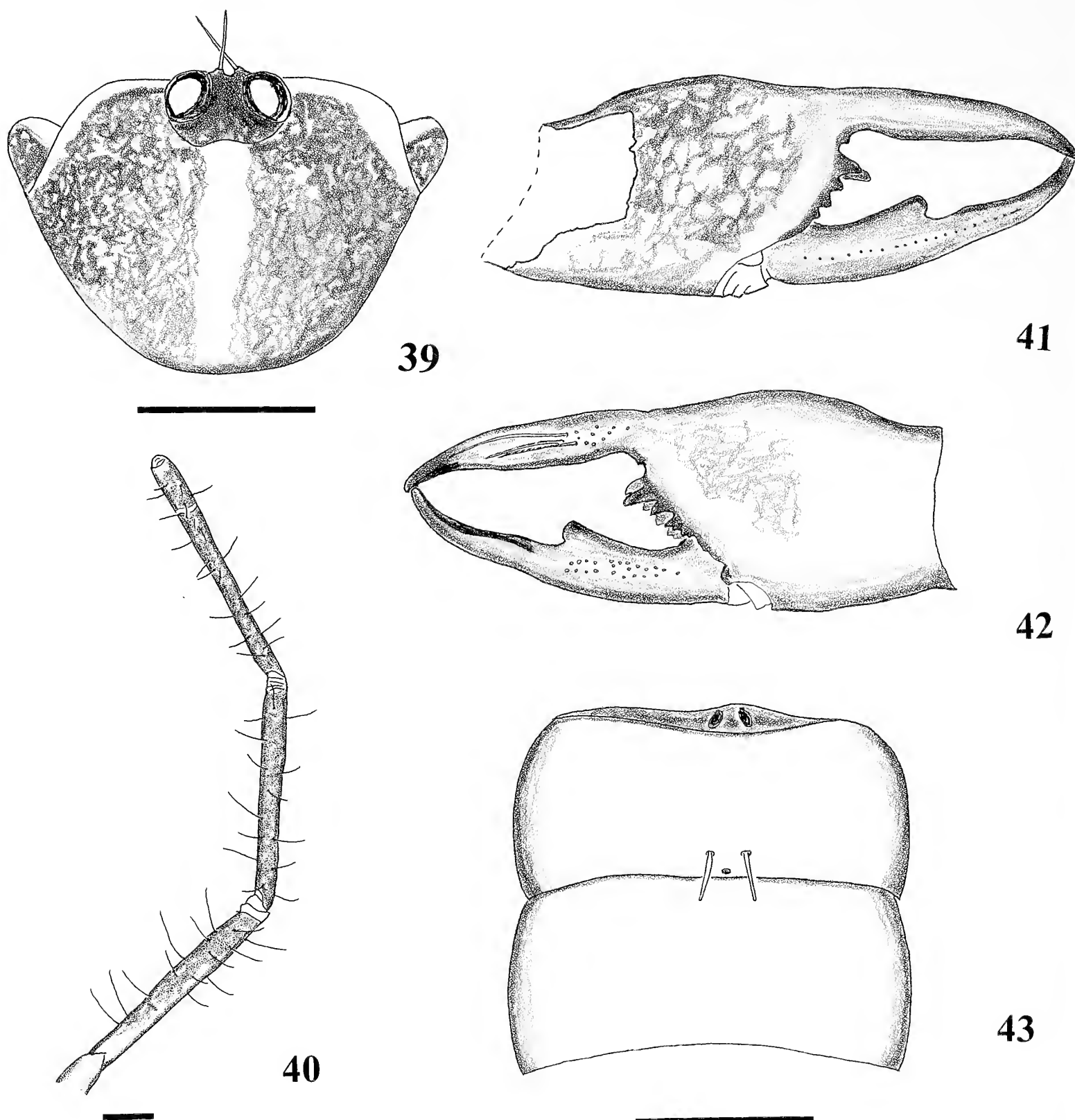
Description.—*Male holotype*: total length 14, chelicera length 3.3, chelicera width 1.3, propeltidium length 1.8, propeltidium width 2.3, palpal length 14, first leg length 7, fourth leg length 16. *Ratios*: A/CP 7.3, CL/CW 2.5, FL/FW 0.7, WFF/FW 1.0, CW/WFF 4.2.

Overall color in alcohol dusky yellow, abdominal tergites darker. Propeltidium dark to dusky with a thin pale oval stripe in middle (Fig. 39). Palpus (Fig. 40) and leg I dusky purple on femur, tibia, metatarsus, and tarsus. Legs II, III, and IV dusky purple on femur, tibia, metatarsus and apical half of tarsus. Mal-leoli white. Fixed finger straight most of the length, curved down slightly at the tip. Ventral edge minutely undulate ending in a shallow trough apically. Mesoventral groove shallow, extending about one half the length of FF on the ventral edge. Movable finger with a single large PT and a small depression anteriorly. No AT or IT. Apical one third with shallow trough on dorsal edge. MST absent. Fondal notch a semicircle rising into the ventral edge of the FF. Fondal teeth graded I, II, III, IV ectally and mesally (Figs. 41 & 42). Flagellum complex typical of *branchi* group with dorsal bristles tubular, medial bristle flattened plumose, ventral series thin, plumose. No papillae on palpal scopae. Two short, thin ctenidia found on posterior margin of 4th abdominal segment (Fig. 43).

Remarks.—The distinctive semi-circular shape of the fondal notch is found in *E. bidepressus* (Muma 1951) of the *branchi* group and in *E. flexacus* (Muma 1963), *E. imperialis* (Muma 1951), and *E. insignitus* (Roewer 1934), all members of the *imperialis* group, suggesting that a revision of both groups might be in order based on this character. *Eremochelis oregonensis* can be distinguished from the closely related *E. bidepressus* by the size of the ctenidia which are short in *E. oregonensis* and long and thin in *E. bidepressus* and the position of the mesal groove. *E. bidepressus* has only been found in Utah.

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We would like to thank those mentioned previously who provided material for examination as well as my colleague, Sandy Brantley, University of New Mexico for use of their collections. Also thanks to John T. Pol-



Figures 39–43.—*Eremochelis oregonensis* new species, male holotype. 39. Male propeltidium, dorsal view; 40. Male right palpus, mesoventral view; 41. Male right chelicera, ectal view; 42. Male right chelicera, mesal view; 43. Male fourth abdominal segment showing ctenidia, ventral view. Scale bar = 1 mm.

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OROBOTHRIURUS ATQUIPA, A NEW BOTHRIURID SPECIES (SCORPIONES) FROM LOMAS IN SOUTHERN PERU

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ABSTRACT. *Orobothriurus atiquipa* new species (Scorpiones, Bothriuridae) from Lomas formations in the coastal desert of southern Perú is described and illustrated. This species belongs to the *alticola* species-group, and within the group, it is closely related to *O. alticola* (Pocock), *O. paessleri* (Kraepelin) and *O. curvidigitus* (Kraepelin). The spine formula (4 + 3) on tarsi III–IV is probably an autapomorphy for the new species. Some features of the habitat (the Lomas formation are green isolates in the coastal desert), as well as a distribution map are provided.

RESUMEN. Se describe *Orobothriurus atiquipa* nueva especie de escorpión Bothriuridae, colectado en una formación de Lomas en el desierto costanero del Sur del Perú. Esta especie pertenece al grupo *alticola*; dentro de éste, las especies más próximas son *O. alticola* (Pocock), *O. paessleri* (Kraepelin) y *O. curvidigitus* (Kraepelin). La fórmula de espinulación tarsal en patas III–IV (4 + 3) es probablemente una autapomorfia de la nueva especie. Se presentan también algunos datos del habitat de *O. atiquipa* (las formaciones de Lomas son verdaderos parches de vegetación dentro del desierto costero), así como un mapa de distribución.

Keywords: Scorpiones, Bothriuridae, *Orobothriurus*, Perú, Neotropics

The genus *Orobothriurus* Maury 1976 (Scorpiones, Bothriuridae) comprises small to medium sized bothriurids, with most species inhabiting high Andean environments above 2,000 m, from Perú to Argentina. The taxon follows very closely the Andean distributional pattern (Maury 1976), also referred to as the “trans-Andean” or “A” corridor (Lourenço 1994). One *Orobothriurus* species was reported to hold the elevation record for the whole order (Polis 1990; Lourenço 1997), and in some cases the genus has been thought to include only high elevation species (Lowe & Fet 2000). The latter statement, however, overlooks the fact that at least one species, *Orobothriurus paessleri* (Kraepelin 1911) was already known to occur near the Pacific coast, in southern Perú (Maury 1976; Dávila Flores 1982). With more materials at hand (Ochoa & Acosta, pers. obs.), it is now clear that this species exists in a very peculiar biotope, the “Lomas”, a plant formation which develops on seawards slopes inside the highly xeric coastal desert. In this paper we describe the second *Orobothriurus* species inhabiting the Lomas, *O. atiquipa* new species, captured

more northerly than *O. paessleri*. The presence of these species at low elevations does not contradict the general Andean pattern, for it should comprise not only the Andean chains proper, but also several associated orographic systems east of the Andes (e.g. sub-Andean and Pampean systems in W and NW Argentina, from where some captures of *Orobothriurus* have been reported; Acosta & Ochoa 2001, as well as the low Coastal Range of Perú and N Chile, where most of the Lomas develop.

Lomas formations extend along the Pacific coast from about Trujillo, Perú (8°S) to the Chilean locality of Coquimbo (30°S) (Ferreira 1986). They are green isolated patches, surrounded by one of the most extreme hot deserts on earth (Péfaur 1981). In the Lomas of Yuta, temperature ranges between 26–28 °C (highest temperatures in summer) and 10–12 °C (lowest temperatures in winter) (Dávila Flores 1982); the annual precipitation (rain plus fog) fluctuates between 125 and 250 mm, while the surrounding areas receive only 20 mm a year (Péfaur 1981). Precipitation is most concentrated in winter, and the vegeta-

tion shows an accordingly remarkable seasonal phenology, caused by the drastic meteorological changes. The winds bring humidity from the sea to the continent. In winter and the beginning of spring (June–October), the fog condenses on the west-facing slopes of the Coastal Range (most abundant at 700–1000 m), enabling the appearance of Lomas vegetation; this phenomenon develops much more strikingly in years when “El Niño” occurs, because of the increase of humidity. In summer, these areas remain relatively free of clouds or fog and the moisture in the air does not condense on the Lomas, but continues its east-ward displacement up to the higher slopes of the Andean Cordillera Occidental (Bowman 1938). In contrast to the plant phenology, many animal communities are more abundant in the dry season, following a sudden increase in September (Péfaur 1981). The insular condition of the Lomas and their seasonality attracted the attention of several researchers, who have carried out many vegetation and faunistic surveys (Aguilar 1964; Dávila 1979; López 1977; López et al. 1978; Péfaur 1981). The scorpion species previously known from Lomas biotopes include the iurid *Hadruides lunatus* (L. Koch 1867), and the bothriurids *O. paessleri* and *Brachistosternus ehrenbergii* (Gervais 1841) (Aguilar 1968; Dávila Flores 1982). The senior author has also collected there some as yet undetermined *Brachistosternus* (*Leptosternus*) species.

With the description of *O. atiquipa* new species, the number of species contained in *Oroborthriurus* is now 11 (Maury 1976; Acosta & Ochoa 2000, 2001). Carinae on metasomal segments are described according to the following nomenclature and abbreviations: DL = dorsal lateral; LSM = lateral supramedian; LM = lateral median; LIM = lateral inframedian; VL = ventral lateral; VSM = ventral submedian; VM = ventral median. Materials examined are deposited at Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN), and Museo de Historia Natural, Facultad de Ciencias Biológicas, Universidad Nacional de San Antonio Abad del Cusco, Perú (MHNC).

***Oroborthriurus atiquipa* new species**

Figs. 1–8

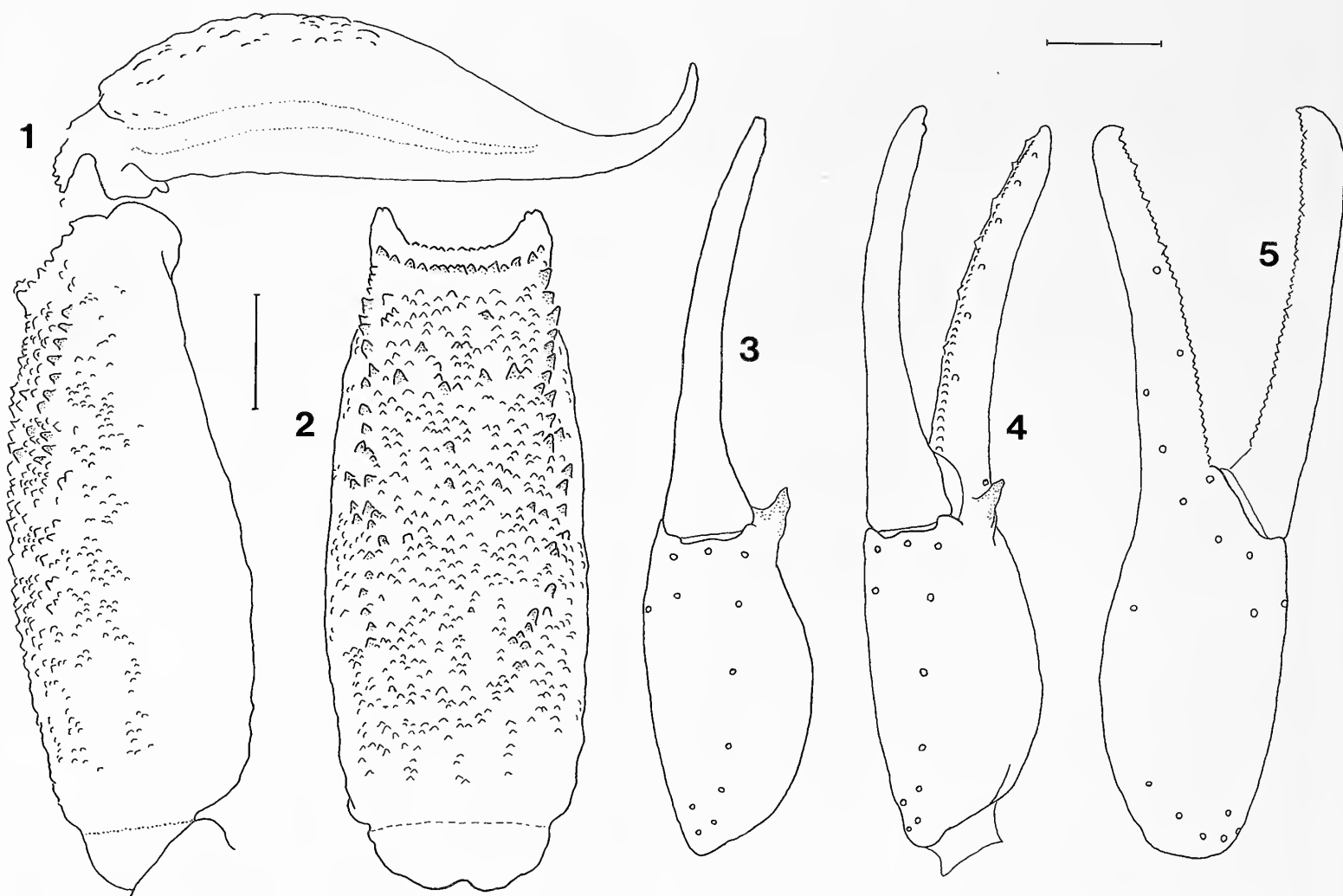
Etymology.—The species name is a noun in apposition, based on the type locality.

Type series.—Holotype ♂ (MACN 10010), 1 ♂ paratype (MHNC): Lomas de Atiquipa (Cerro Lloque, 950 m, 15°45'S 74°22'W), Departamento Arequipa, Perú (Fig. 9), 13 September 1999, H. Zeballos & R. Gutierrez coll.

Diagnosis.—Species belonging to the *alticola* species-group as defined by Acosta & Ochoa (2001). Within the group, *O. atiquipa* new species shows the closest affinities with *O. alticola* (Pocock 1899), *O. curvidigitus* (Kraepelin 1911) and *O. paessleri* (Kraepelin 1911), which have been already determined to form a subgroup in the *alticola* group. This subgroup is characterized, among other features, by the shape of the hemispermatophore lamina: basal portion substraight, and a reduced, S-curved tip (Acosta & Ochoa 2001). The frontal crest of the lamina of *O. atiquipa* new species is proportionally longer than its closest relatives, and the whole lamina has a more slender appearance. The pigmentation pattern of the new species is similar to most members of the *alticola* group (axial clear stripe on mesosoma, ventral dark line on metasoma); however, unlike the typical pattern in the group, on metasomal segments I–III the ventral line has irregular expansions and joins distally to the ventrolateral pigment (in most species the line remains separate all along the metasoma). The dense and irregular ventral granulation of metasomal segment V, and the tarsal spine formula on legs III–IV (most tarsi with 4 + 3 spines) are unique of *O. atiquipa* new species in the whole genus; as a (hitherto) constant generic feature, all remaining *Oroborthriurus* bear 3 + 3 ventral spines on telotarsi III–IV, so that this peculiar character state for the new species is probably an autapomorphy. The trichobothrial pattern agrees with the group definition, but is closer to *O. alticola* in subtle details: Et₃ slightly more proximal than Est, Esb above Eb₂.

Description.—Medium sized scorpions; females unknown. Ground color straw-yellowish, with brown dense reticle on carapace, mesosomal tergites, metasoma and legs; venter depigmented, pectines whitish.

Pigment pattern.—Carapace densely pigmented, especially the anterior third, with pigment filling up to the frontal border; ocular mound even darker. Tergites I–VI with two large paramedian pigment areas, extending to the pretergite but not reaching the lateral edge-

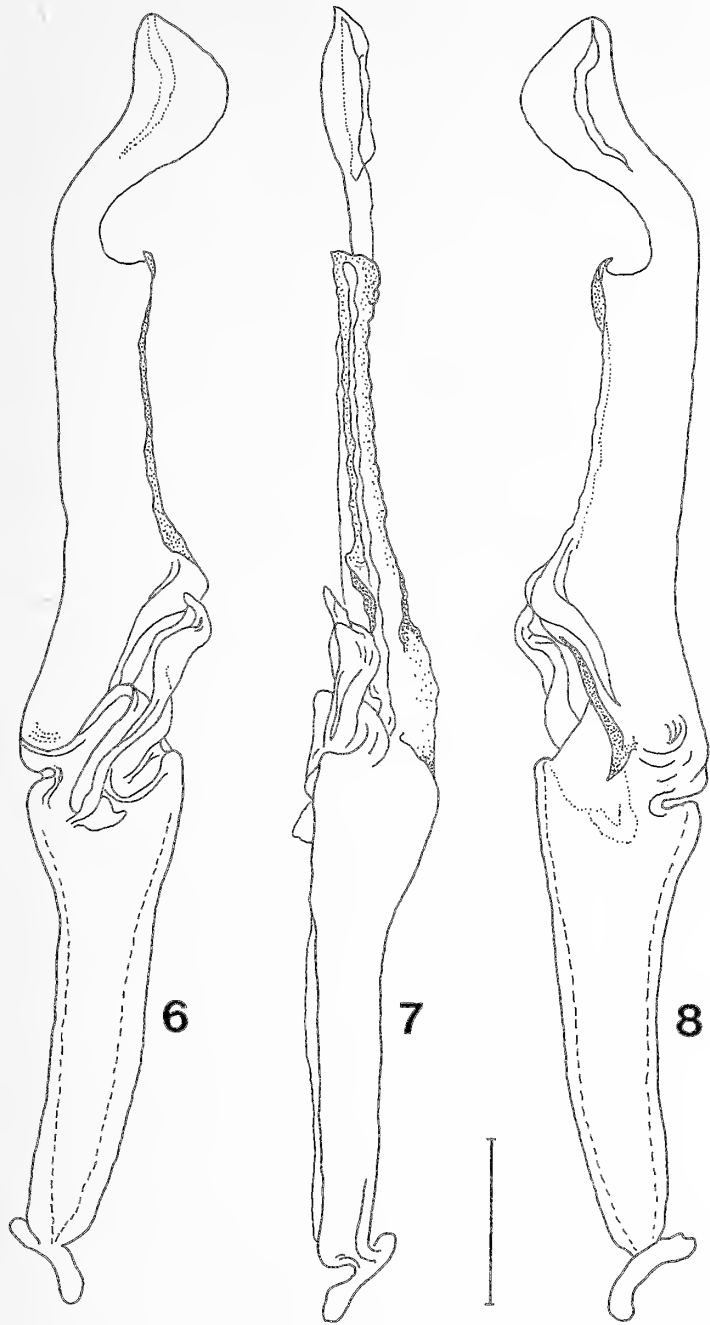


Figures. 1–5.—*Orobothriurus atiquipa* new species, holotype male (MACN); 1. Metasomal segment V and telson, lateral view; 2. Metasomal segment V, ventral view; 3–5. Right pedipalp chela; 3. Ventral view; 4. Ventromedial view; 5. Lateral view. Scale bars = 1 mm.

es; they leave small, irregular clear areas inside of the pigmented sector, forming a “crescent-shaped” figure on each side. A median unpigmented stripe between these pigmented areas constitutes a longitudinal clear stripe along the mesosoma (in the holotype it is 14.3 % of the tergite width, 11.9 % in the paratype). On tergite VII the lateral pigment is fainter and the median clear stripe is much less defined. Metasomal segments I–III: one dorsal irregular spot, roughly shield-like (on segment I it is divided by a clear median line); segment IV with an elongated spot, less defined. Laterally with a dense reticle, reaching the telescopic part of each segment; it is darker towards the distal portion. Ventrally with a median stripe, wide and irregular on segments I–III (reticular expansions join to thin paramedian lines), quite sharp on segment IV; the median stripe joins distally the lateral pigment through reticular pigment, very faint on segment IV. Metasomal segment V: on lateral view, three longitudinal, reticulate major stripes (dorsolateral, lateral, ventrolateral) join at the caudal end; ventral face with a thin me-

dian line, thickened posteriorly but not joining the ventrolateral pigment. Chelicerae with very faint reticle. Pedipalps: dorsal face of femur pigmented on its borders and on the distal quarter, leaving a large elongated clear area on the median portion; patella densely reticulat-ed; chela with irregular faint lines along the hand, joining at the base of fingers. Prolaterally, legs with reticular spots.

Morphology: Tegument finely granular, granulation more pronounced near the front median edge of carapace and the laterals of tergites. Front edge of carapace with a slight median prominence. Tergite VII granulous, with four carinae of granules increasing in size posteriorly. Sternites I–II smooth, III–IV with slight granulation on the posterior border, V with dense granulation on the median third. Metasomal segments I–IV. DL carinae complete, the posterior granule slightly larger than the rest. LSM carinae complete, conspicuously granulous on segment I, smaller granules on segments II–IV. LIM carinae limited to the posterior third, represented by sparse granulation on segments III–IV. VL carinae less de-



Figures. 6–8.—*Orobethriurus atiquipa* new species, left hemispermatotheca of the holotype; 6. Internal view; 7. Frontal view; 8. External view. Scale bar = 1 mm.

finer and sparsely granular, granulation decreases towards segment IV. VSM carinae lacking, they are replaced by scattered granulation (dense on segment I, much less evident on segments II–IV). Metasomal segment V. DL carinae complete, 4–5 proximal granules slightly larger. LM carinae represented as fine sparse granulation, especially on the distal half. Ventral surface scabrous, with large granules densely covering the segment: VL carinae are discernible on the distal half, but VSM and VM carinae disappear among the abundant ventral granulation (on the male paratype a faint VM can be distinguished). Number of VSM setae on metasomal segments I–IV: 3–3–3–4 pairs. Telson slightly granular, low (length / height ratio: 4.0 in the holotype,

Table 1.—Measurements (mm) of the holotype male of *Orobethriurus atiquipa* new species.

Total length	31.3
Carapace: length	3.7
anterior/posterior width	3.9/2.7
Mesosoma, length	7.3
Metasoma, length	20.3
Metasomal segment I, length/width	1.9/2.4
Metasomal segment II, length/width	2.4/2.2
Metasomal segment III, length/width	2.5/2.2
Metasomal segment IV, length/width	3.2/2.1
Metasomal segment V, length/width/height	5.1/2.1/1.9
Telson, length	5.2
Vesicle, length/width/height	4.1/1.7/1.3
Sting, length	1.1
Pedipalp, total length	13.2
Femur, length/width	3.5/0.9
Patella, length/width	3.7/1.1
Chela, length/width/height	6.0/1.3/1.5
Movable finger, length	3.5

4.3 in the paratype). Pedipalps slender, fingers proportionally long (chela length / width ratio: 4.6 in the holotype, 4.7 in the paratype); acute spine-shaped apophysis on the prolateral side of hand. Trichobothrium Et₃ slightly more proximal than Est; Esb above Eb₂, it is slightly displaced to Eb₁ in the paratype. Legs: telotarsi III–IV with 4 + 3 ventral spines (only the left tarsus IV of holotype with 3 + 3). Number of pectinal teeth: holotype with 24–23, paratype 24–24. Hemispermatotheca slender, lamina straight, except of the apex, S-curved; distal crest curved, parallel to the abfrontal border; frontal crest longer than the half of the lamina, internal border almost smooth, external slightly undulated. Lobe region all like the *alticola* group.

Habitat.—The species is only known from the type locality, a Lomas formation on the coastal desert of northern Departamento Arequipa, Perú (Fig. 9). Specimens were captured in pitfall traps. The main plant physiognomy in the capture site is that of a shrubland (*Duranta armata* Moldenke, *Citharexylum flexuosum* (Ruiz Lopez & Pavon) D. Don, and *Heliotropium arborescens* L. are the most characteristic species), but also gramineae and small forests of “tara” (*Caesalpinia spinosa* (Molina) Kuntze), “arrayán” (*Myrcianthes ferreryae* (Mc Vaugh) Mc Vaugh) and *Acacia macracantha* Humboldt & Bonpland ex Willdenow occur there (H. Zeballos pers. comm.).

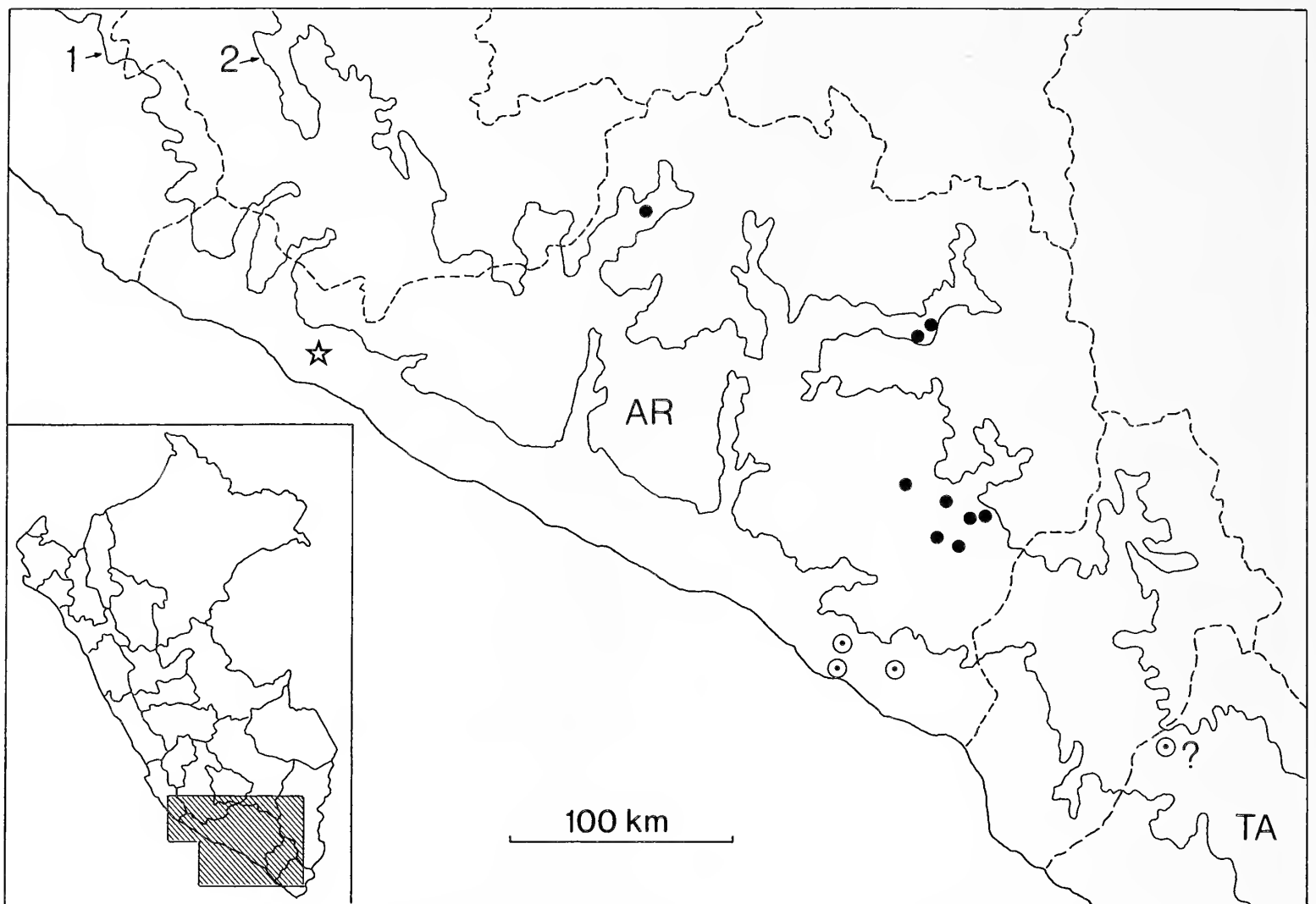


Figure. 9.—Records of three *Orobthriurus* species in southern Perú: *O. atiquipa* new species (star), *O. curvidigitus* (black dots), *O. paessleri* (open circles). Solid lines: upper limits of the coastal desert (1 = circa 1000 m a.s.l.) and the “serrania esteparia” (2 = ca. 3800 m). Dashed lines: administrative boundaries of Departamentos (AR = Arequipa, TA = Tacna). Inset: location of the represented area in Perú.

The geographically nearest *Orobthriurus* species is *O. curvidigitus*, with captures between 2300 and 3600 m at Cotahuasi, in the Colca canyon, and in several localities around Arequipa (Fig. 9); however, this species does not occur in the coastal desert but in a quite different ecoregion, the “Serrania Esteparia” (Brack 1986). The nearest desert species is *O. paessleri*, also captured in Lomas biotope (Lomas de Mejía and Yuta, southern Departamento Arequipa), 280 km away from Atiquipa. The desert in between might act as a barrier separating these two related species. The isolation of each Loma patch and the high degree of endemism in these formations may suggest *O. atiquipa* new species to be endemic of its capture site, but this should be supported by further samplings.

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REDESCRIPTION OF *METACLEOBIS FULVIPES* ROEWER FROM BRAZIL (SOLIFUGAE, MUMMUCIIDAE)

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ABSTRACT. The species *Metacleobis fulvipes* Roewer 1934 (Solifugae, Mummuciidae), previously known only from the male holotype, is redescribed based on the holotype and other male and female specimens. Illustrations of the main diagnostic characters are provided, and new occurrences of this species in Brazil are reported. Some behavioral observations of one individual kept in a terrarium are given.

RESUMO. A espécie *Metacleobis fulvipes* Roewer 1934 (Solifugae, Mummuciidae), conhecida previamente apenas pelo holótipo macho, é redescrita a partir do holótipo e de outros exemplares machos e fêmeas. Ilustrações dos principais caracteres são fornecidas e novas ocorrências da espécie no Brasil são registradas. São descritas observações comportamentais feitas a partir de um indivíduo mantido em terrário.

Keywords: Solifugae, Solpugida, Mummuciidae, taxonomy, Brazil

The geographic distribution, systematics and general biology of the South American Solifugae are poorly known. Research on Solifugae has been neglected by researchers, perhaps due to the difficulty in collecting these arachnids. Important studies on South American species have been done by Maury (1970, 1982, 1984, 1987, 1998) who published a series of papers on Solifugae systematics, with comments on their biogeography. In another important paper, Roewer (1934) described many species of Solifugae from the Neotropics, although most of them have very short and not very informative descriptions. This is the case with *Metacleobis fulvipes* Roewer 1934, in which the description is imprecise and based on a single male. Here, *Metacleobis fulvipes* is redescribed based on the holotype and on other male and female specimens, with comments on some behavioral aspects of one individual kept in a terrarium.

METHODS

The terms “bristles”, “setae” and “spines” are used according to Muma (1951). For instance, some of these structures bear a bifurcation at the tip and are called “bifid bristles”. Cheliceral teeth are also named according to Muma (1951), in which sizes of cheliceral

teeth are ordered with Roman numerals, size I being larger than II, and so on. The leg spination formulae are used as in Maury (1982) and the podomere terminology is used according to Shultz (1989). The term “ctenidia” is used as in Maury (1984).

Some telotarsi were cleared and stained according to Maury (1982), with the following modifications: the legs were placed in hot (near boiling) 1N NaOH solution, then transferred to Giemsa’s staining solution and washed in 80% ethanol to remove the excess stain.

We examined specimens from the following collections: Senckenberg Museum, Frankfurt, Germany (SMF); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (MCTP); Universidade Federal do Mato Grosso, Cuiabá, Brazil (UFMT).

Family Mummuciidae

Genus *Metacleobis* Roewer 1934

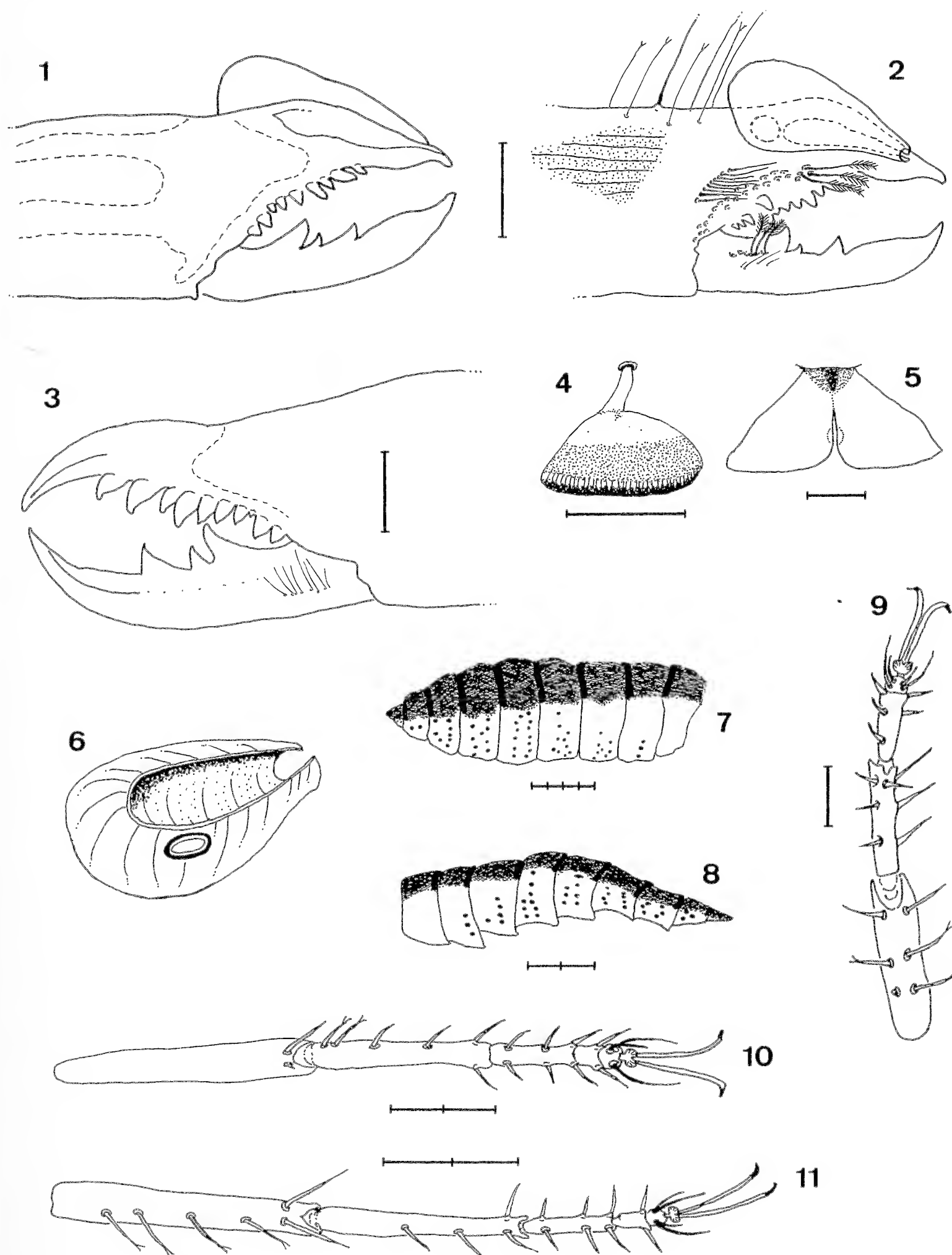
Metacleobis fulvipes Roewer 1934

Figs. 1–12

Metacleobis fulvipes Roewer 1934: 589–590, fig. 333c; Zilch, 1946: 150; Muma, 1976: 24; Maury, 1984:75, figs. 4–5.

Types examined.—Male holotype (SMF

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Figures 1-11.—*Metacleobis fulvipes*. 1. Right chelicera, ectal view, of male. 2. Left chelicera, mesal view, of male; only some of the plumose setae are depicted. 3. Left chelicera, ectal view, of female. 4. Left malleolus V of male holotype. 5. Genital operculum of female. 6. Schematic representation of right flagellum, showing the longitudinal lateral opening and the attaching ring, both in the ectal face. 7. Right pleurites of female; note the assembly of dark-brown sockets on the white portion of pleurites. 8. Left pleurites of male; 9. Left leg II of male. Note the bifid spines on the tibia (one is broken). 10. Left leg IV of female; note the bifid spines on the basitarsus. 11. Right leg IV of male; note the bifid spines on the tibia. Scale: each division = 0.50 mm.

4556), from Cuiabá, State of Mato Grosso, Brazil, (15°35'S, 56°05'W), C. Roewer coll. 1933.

Other material examined.—10♂ and 3♀ (MZUSP 15153, MZUSP 15154), from Serra da Mesa, State of Goiás, Brazil (14°17'09"S, 49°55'03"W), G. Skuk coll., 31 May 1996; 1♂ (MCTP 0002), A. Lise coll. 18 July 1992 and 1♀ UFMT, M. Carvalho coll. March 1996, both from Chapada dos Guimarães, State of Mato Grosso, Brazil (15°26'S, 55°45'W).

Diagnosis.—*Metacleobis fulvipes* is the only species of Mummuciidae with cheliceral dentition as depicted in Figs. 1–2 (males) and Fig. 3 (females).

Description of male.—Color in 80% ethanol: Prosoma: propeltidium brown with lighter regions at the anterior border, on each side of ocular tubercle and on two posterior-lateral areas. Eyes and ocular tubercle dark-brown. Peltidium white, posterior border dark-brown. Parapeltidium, mesopeltidia and metapeltidium similar to opisthosomal tergites. Chelicerae brown, with three longitudinal pale-brown stripes on ectal face joined dorsally above the fondal teeth. Pedipalps and legs brown, ventral face pale-brown. Malleoli pale-brown with distal region darker (Fig. 4), a color pattern more distinguishable in the two distal malleoli (IV and V). Opisthosoma: lateral borders of tergites white, one wide dark-brown stripe in the central half; this stripe is darker near posterior border of tergites. Brown bifid setae with brown sockets if in white area of the tergites, and white sockets if in the dark-brown area. Pleurites white (Fig. 8), dark-brown dorsal coloration occupying about one third of the width in the 5 proximal pleurites and almost half in the others. Pale-brown translucent bifid bristles on the white portion of pleurites with dark-brown sockets, arranged as in Fig. 8. Sternites pale brown, lateral borders brown. Vestitural bristles translucent pale-brown. Post-spiracular sternites 1–4 with about 25, 20, 10 and 5 brown spots, respectively, which include the sockets of some bifid bristles.

Morphology and chaetotaxy: Prosoma: propeltidium slightly wider than long, separated from lateral lobes by dorsal grooves and covered by short bristles and bifid setae. Ocular tubercle prominent with bifid setae oriented forward. Distance between the eyes slightly

wider than one eye diameter. Peltidium narrow, with a transverse row of bifid setae. Parapeltidium smooth. Mesopeltidium wider than long and semicircular with several bifid setae on posterior border. Metapeltidium wider than long with several bifid setae. Chelicerae: (Figs. 1 & 2) stridulatory apparatus in mesal face with six or eight parallel narrow grooves; ectal face bears several short bristles and several bifid setae; movable finger mesal face with some setae and plumose setae; dentition: one anterior, one intermediate and one principal tooth graded in size respectively II, III, I; fixed finger on mesal face with two rows of plumose setae parallel to the teeth and one smaller row of setae behind (Fig. 2); dentition: two anterior teeth, one intermediate and one principal tooth, graded in size from distal to proximal II, I, III, I (Fig. 1); five ectal fondal teeth, graded in size from distal to proximal I, II, III, II, II, or six teeth graded in size I, II, IV, II, II, III (the third distal may be vestigial); usually three mesal fondal teeth, graded in size from distal to proximal I, II, III, the first distal separated from others by a diastema, the most proximal (third) may be lacking or a fourth and smallest proximal mesal fondal tooth may be present. Flagellum thin (Figs. 1 & 6), translucent tear-drop-shaped vesicle, compressed and with a longitudinal ectal opening (in the face adjacent to the chelicera), which extends from near the base to tip of flagellum. Base of flagellum is a sclerotized ring placed posteriorly on ectal face. Flagella filled with a white viscous substance. Pedipalps with tarsi immovable, without spines, densely covered by differentially sized bifid bristles, with some very long setae on tibiae and patellae (about twice the length of pedipalpal patella). Legs (Figs. 9 & 11) with several differentially sized bifid bristles and some bifid setae. Some very long setae on the dorsal surfaces (about twice the length of leg IV basitarsus). Leg I thin, without telotarsal claws and spines. Legs II and III (Fig. 9): tibiae (spination formulae) with 1.1, 1.2, 2 or 2.2 ventral bifid spines and a distal pair of ventral spines; basitarsus with three retrolateral spines and 1.1.2 ventral spines; telotarsi two-segmented, 1.1.2/2.2 or 1.2.2/2.2 ventral spines. Leg IV (Fig. 11): tibiae with an anterior row of 1.1, 1.1.1, 1.1.1.1 or 1.1.1.1.1 ventral bifid spines and a distal pair of ventral spines; basitarsus with or without a proximal anterior row of 1.1

Table 1.—Morphometric characters of *Metacleobis fulvipes*. Measurements are in millimeters (except propeltidium length/width ratio) and were recorded as described in Muma (1951).

Morphometric character	Holotype	Males (n = 12)	Females (n = 4)
Total length	11.50	9.35–11.50	9.80–16.50
Cheliceral length	2.75	2.15–2.75	2.95–3.76
Cheliceral width	1.05	0.75–1.05	1.15–1.28
Propeltidium length	1.80	1.55–1.80	1.70–2.04
Propeltidium width	2.40	1.80–2.40	2.30–2.96
Propeltidium length/width ratio	0.75	0.82–0.75	0.74–0.69
Pedipalp length	6.75	6.00–7.00	5.75–7.10
Leg I	6.05	4.35–6.50	4.75–6.10
Leg IV	11.30	9.30–11.30	9.10–11.50

ventral bifid spines and with 1.1.2 or 1.1.1.2 ventral spines; telotarsi three-segmented, 2.2.2/2/1, 2.2.2/2/2 or 2.2.2/2/2.2 ventral spines. Spines of the distal tarsomere in legs II, III and IV are longer and thinner than the others. Malleoli as in Fig. 4. Opisthosoma: tergites wider than long, rounded borders, covered by several bifid bristles. Pleurites, 1–5 wider than long, 6–8 longer than wide. Sternites wider than long, densely covered by bifid bristles. Genital operculum with central longitudinal opening. Posterior border of post-spiracular sternite 2 with a row of about 50 ctenidia, thinner and more rigid than the sternite bifid bristles. Morphometric characters in Table 1.

Description of female.—Similar to male, but with the following differences.

Color in 80% ethanol: Opisthosomal pleurites with a pattern of dark-brown sockets arranged as in Fig. 7. Post-spiracular sternites without conspicuous brown spots.

Morphology and chaetotaxy: Prosoma: propeltidium wider than long. Bifid setae more abundant than in male. Eyes separated by three times one eye diameter. Chelicerae (Fig. 3): fixed finger with two anterior, one intermediate and one principal tooth, graded in size respectively II, I, III, I; five ectal fondal teeth graded in size from distal to proximal I, II, III, I, II or six graded I, II, III, IV, II, III and three mesal fondal teeth similar to male. Leg IV (Fig. 10): tibiae with an anterior row of 1.1 or 1.1.1.1 ventral bifid spines and a distal pair of ventral spines; basitarsus with a proximal anterior row of 1.1 ventral bifid spines and 1.1.2 or 1.1.1.2 ventral spines (Fig. 10); telotarsus with 2.2.2/2/2, 2.2.2/2/1.2 or

2.2.2/2/2.2 ventral spines. Opisthosoma: posterior border of post-spiracular sternite 2 with a row of about 50 ctenidia, thinner and more rigid than the sternite bifid bristles. Genital operculum prominent, fan-shaped, round-bordered, with central longitudinal opening (Fig. 5). Morphometric characters in Table 1.

Distribution.—*Metacleobis fulvipes* was described from Cuiabá, State of Mato Grosso, but the maps of geographic distribution of Solifugae published by Savory (1964) and Punzo (1998) do not mention the occurrence of this species. The new records of *Metacleobis fulvipes* are from Serra da Mesa, State of Goiás and Chapada dos Guimarães, State of Mato Grosso, both in Brazil.

Biological observations.—There are few papers describing the behavior of Solifugae. One of us (L.S.R.) maintained a female of *Metacleobis fulvipes* from Serra da Mesa (Fig. 12) for 81 days in 1996 in a glass box terrarium with dimensions (cm) 30 × 20 × 20 high. The substrate was sand with some surface plant leaves, small stones and pieces of wood. The specimen exhibited diurnal activities of walking and burrowing, and during the night, the specimen remained inactive under the same piece of wood. “Drowning” behavior was observed as described for some North American species by Muma (1967). The female was submerged in water for two hours and afterwards transferred to the terrarium. After drying, the specimen gradually recovered its normal mobility and activities. The specimen apparently exhibited some characteristics of “taming” (Muma 1966), since it survived for 81 days but never ate any items offered, i.e., termites, ants, small beetles and



Figure 12.—Photograph of a female of *Metacleobis fulvipes* maintained in a terrarium. Total length of the individual = 9.80 mm (Photograph by Dr. Ricardo Pinto-da-Rocha).

uncooked beef. Moreover, it did not show aggressive behavior against the living insects offered or against the manipulations of the observer.

DISCUSSION

The present redescription of *Metacleobis fulvipes* permits a more precise identification of this species based upon male and female specimens. The original description (Roewer 1934) was based on a single male, is very brief and provides imprecise information. For example, the holotype of *Metacleobis fulvipes* actually bears three mesal fonal teeth on the fixed cheliceral finger instead of two, as incorrectly depicted in Roewer's drawing (Roewer 1934, fig. 333c). An important character not mentioned by Roewer is the lateral opening placed in the ectal face of the flagellum. This opening is different from the opening found in the flagella of Ammotrechidae, which is located on the mesal face. Other systematic features of *M. fulvipes* such as pilosity, ctenidia, dark-brown sockets in opisthosomal pleurites, morphometric characters and female characters are newly described for this species.

Roewer (1934) relied heavily upon telotarsal spination patterns to segregate *Metacleobis* from other genera. However, this character system is a poor taxonomic discriminator and Maury (pers. comm., 1997, 1998) has sug-

gested to us that it is not possible to satisfactorily distinguish between the 10 named genera currently attributed to the Mummuciidae, and that a detailed systematic revision is needed to elucidate the relationships of the constituent taxa. Therefore, we have maintained the genus *Metacleobis* until such a review is undertaken.

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We thank the following curators who kindly provided material: Dr. Manfred Grasshoff (SMF), Dr. Arno A. Lise (MCTP) and Dr. Rosina Miyazaki (UFMT). We also thank Dr. Antônio D. Brescovit, Dr. Carlos R.F. Brandão, Dr. Ricardo Pinto-da-Rocha and Dr. Rogério Bertani for their useful suggestions. Lincoln Suesdek Rocha would like especially to thank, *in memoriam*, Dr. Emilio Maury (deceased July, 1998) not only for critical reading of the redescription of *Metacleobis fulvipes*, but also for the friendship and invaluable help during the short period I worked at Maury's laboratory.

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A CLADISTIC ANALYSIS OF THE CYPHOPHTHALMID GENERA (OPILIONES, CYPHOPHTHALMI)

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ABSTRACT. A phylogenetic analysis of the genera of Cyphophthalmi is undertaken by studying 32 morphological characters in 43 species representing all families and most genera. The analysis is complemented with a molecular analysis using 18S rRNA and 28S rRNA sequence data of twelve cyphophthalmid species representing ten genera. The Cyphophthalmi are monophyletic, as are the families Stylocellidae and Pettalidae. However, the families Sironidae, Ogoveidae, and Neogoveidae are not monophyletic. Relationships among families need more data, but molecular characters strongly support the monophyly of Troglosironidae + Neogoveidae. Rooting the cyphophthalmid tree by using sequence data of one Eupnoi, one Dyspnoi, and one Laniatores results in two alternatives, one proposing a sister group relationship of Stylocellidae to the remaining taxa, or alternatively Pettalidae (with *Suzukielus*?) as sister group of the remaining cyphophthalmids. The position of *Troglosiro*, *Suzukielus*, *Metasiro*, *Huitaca*, and the epigeal “*Neogovea*” *mexasca* are re-evaluated and discussed.

Keywords: Cyphophthalmi, systematics, molecular data, morphological data, cladistics

The arachnid suborder Cyphophthalmi contains about 115 described species (Giribet 2000) of mostly inconspicuous opilionids. The suborder is the smallest of the four opilionid suborders (the other three being Eupnoi, Dyspnoi, and Laniatores according to Giribet et al. 1999, 2002). The taxonomy of the group has changed considerably in recent times, especially with the work of Shear (1980, 1993a). The first attempt to systematize the suborder was the monographic work of Hansen & Sørensen (1904), which divided the single family Sironidae into two subfamilies, named Stylocellini (sic) and Sironini (sic). The Stylocellini contained the genera *Stylocellus* Westwood 1874, *Ogovea* Hansen & Sørensen 1904, and *Miopsalis* Thorell 1890. The subfamily Sironini contained the genera *Pettalus* Thorell 1876, *Purcellia* Hansen & Sørensen 1904, *Siro* Latreille 1796, and *Parasiro* Hansen & Sørensen 1904. One of the main characters to establish this classification is the presence of mobile coxae II in Sironini, while it is fused to coxae III and IV in Stylocellini. This classification remained in place until the seminal studies of Shear (1980, 1993a) who established the new classification system of the Cyphophthalmi, with two infraorders, Temperophthalmi Shear 1980 and Tropicoph-

thalmi Shear 1980 corresponding to the subfamilies Sironini and Stylocellini of Hansen & Sørensen (1904). The Temperophthalmi contain a single superfamily, Sironoidea Simon 1879 with three families, Troglosironidae Shear 1993, Sironidae Simon 1879 and Pettalidae Shear 1980. The Tropicophthalmi include two superfamilies, Stylocelloidea Hansen & Sørensen 1904 with the single family Stylocellidae, and the Ogoveoidea, with the families Ogoveidae Shear 1980 and Neogoveidae Shear 1980.

The new classification of Shear (1980) was based on a cladistic (non-numerical) analysis of all known cyphophthalmid genera. However, the use of generic characters in many cases, and the discovery of new cyphophthalmid species since the study of Shear (1980) made us reevaluate the relationships among cyphophthalmid taxa by selecting exemplar species (Prendini 2001). With this aim, we have coded a morphological matrix including representatives of most cyphophthalmid genera, with the exception of *Odontosiro* Juberthie 1961, *Tranteeva* Kratochvíl 1958, *Manangotria* Shear & Gruber 1996, and *Ankaratra* Shear & Gruber 1996, for which we were unable to examine material. The remaining genera were represented by one or more species,

including the type species whenever possible. We have also included representatives of some new taxa such as two putative species of *Miopsalis*, a new species of *Fangensis*, one pettalid species from Western Australia ("Pemberton"), and a new species of *Ogovea*.

The morphological study has been complemented with a molecular analysis of twelve cyphophthalmid species, representing the families Stylocellidae, Neogoveidae, Troglosironidae, Pettalidae, and Sironidae. The sequence data consists of complete 18S rRNA sequences and the D3 region of the 28S rRNA gene. Representatives of the Eupnoi, Dyspnoi, and Laniatores are used as outgroups in the molecular analysis.

METHODS

Abbreviations.—Specimens are lodged in the following institutions: American Museum of Natural History, New York (USA) = AMNH. Australian National Insect Collection, Canberra (Australia) = ANIC. The Natural History Museum, London (UK) = BMNH. James Cockendolpher private Collection, Lubbock (USA) = CCol. Field Museum of Natural History, Chicago (USA) = FMHD. Field Museum of Natural History, Arachnid collection, Chicago (USA) = FMAC. Museo Civico di Storia Naturale 'Giacomo Doria', Genova (Italy) = MCSN. Museum of Comparative Zoology, Harvard University, Cambridge (USA) = MCZ. Muséum d'histoire naturelle, Genève (Switzerland) = MHNG. Natal Museum, Pietermaritzburg (South Africa) = NMSA. South African Museum, Cape Town (South Africa) = SAM. Senckenberg Museum, Frankfurt am Main (Germany) = SMF. Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Berlin (Germany) = ZMB. Zoological Museum, University of Copenhagen (Denmark) = ZMUC. Western Australian Museum, Perth (Australia) = WAM.

Morphological data.—Material of over 90 species of cyphophthalmids (some undescribed) has been examined, and 43 of these species have been chosen to represent the maximum diversity within the group. All the species included in the analysis have been checked directly from specimens except for *Fangensis leclerci* and *Metagovea disparunguis* for which we have not been able to locate the types from the Rambla collection, or the

Rosas Costa collection respectively, and therefore they are based on literature sources (see Appendix 1).

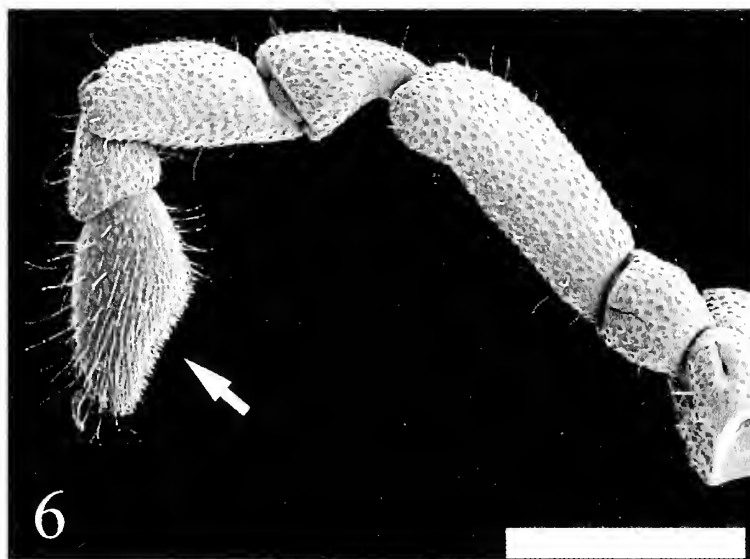
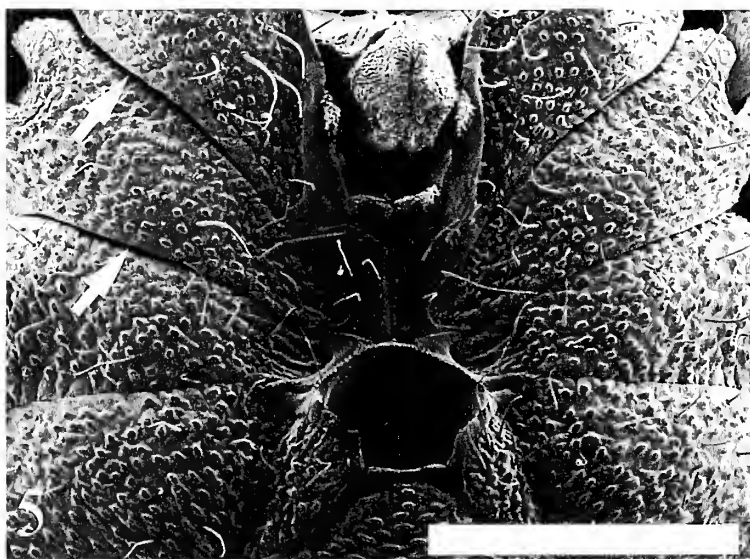
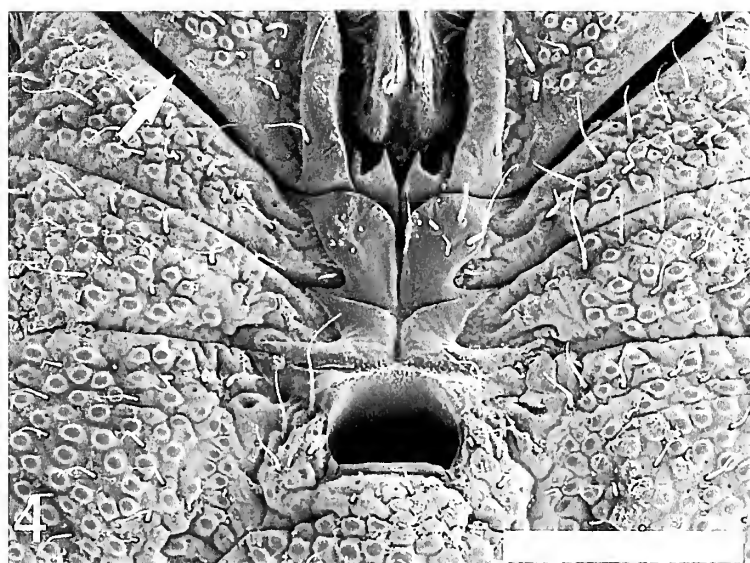
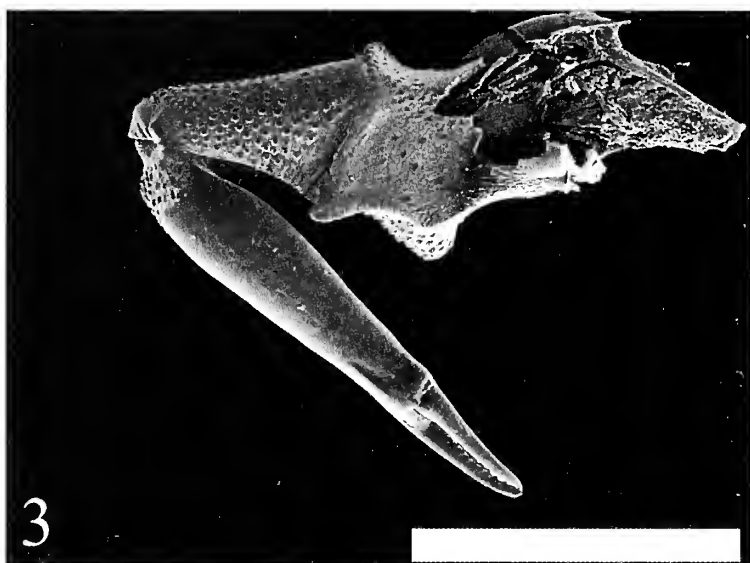
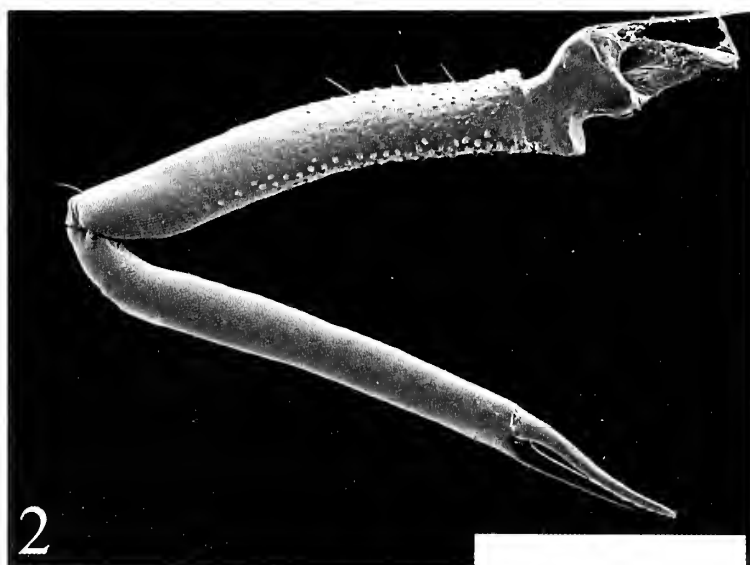
The morphological data matrix has been compiled in NDE v. 0.4.8 (Page 2000), and comprises 32 somatic and sexual characters. All characters are treated as unordered, and equally weighted. The character description and comments refer to the species used in this data matrix (Appendix 2). When relevant character states appear in species not represented in the matrix, those are discussed in the character description.

Morphological characters.—1. *Eyes: absent (0), present (1)*: The presence of eyes in cyphophthalmids of the genus *Stylocellus* has been recently discussed elsewhere (Giribet et al. 2002; Shear 1980, 1993b). No polarity has been assumed.

2. *Ozophore position: type 1 (0), type 2 (1), type 3 (2)*: Juberthie (1970b) categorized three types of ozophores according to the position on the carapace, since it is commonly used for species descriptions. Type 3 shows a dorsal position, as exemplified by *Speleosiro*, while the other two types show a lateral position, with type 1 being completely lateral (Juberthie 1970b: fig. 2a) and type 2 being slightly raised on the carapace (Juberthie 1970b: fig. 2c). The position of the ozophore shows sexual dimorphism in certain species of the genus *Parapurcellia*, but not in the species here used.

3. *Attenuate chelicerae: absent (0), present (1)*: Cyphophthalmid chelicerae are a set of complex characters, perhaps displaying two extreme forms, a robust type found in many sironids, and a very special type, called attenuate type, where the distal cheliceral segment tapers, and the movable finger is extremely small. This condition is found in the members of the genus *Neogovea*, in *Huitaca ventralis* (Fig. 1), and *Pettalus cimiciformis*. However, the cheliceral type of "*Neogovea*" *mexasca* (Fig. 2) is not considered attenuate; it is an elongated type of chelicerae, but does not fit the description here used for the attenuate type. A similar condition is found in some stylocellid chelicera, that even though tapering, they do not have a reduced mobile digit.

4. *Distal segment of chelicerae ornamented: absent (0), present (1)*: The distal segments of the chelicerae are smooth in most cyphophthalmids, but it is completely or partially ornamented in *Stylocellus* (Fig. 3), *Fan-*



Figures 1–6.—1. Attenuate left chelicera of *Huitaca ventralis*; 2. Left chelicera of “*Neogovea*” *mexasca*; 3. External view of left chelicera of *Stylocellus ramblae* showing the dorsal crest and the two ventral protuberances of the basal segment, and the ornamentation near the base of the distal segment; 4. Male ventral thoracic complex of *Metagovea philipi*, with arrowhead showing separation between coxae I and coxae II; 5. Female ventral thoracic complex of “*Neogovea*” *mexasca* with arrowheads showing separation between coxae I, coxae II, and coxae III; 6. Leg I of *Paragovia sironoides* showing the subapical modification of tarsus I where sensory hairs concentrate. Scale bars = 200 μm (Fig. 4), 400 μm (Fig. 5), 500 μm (Figs. 1–3, 6).

gensis (Rambla 1994: Plate II, fig. 1), and *Miopsalis*.

5. *Ornamentation of the distal cheliceral segment: only ornamented at the base (0), mostly ornamented (1)*: Within the members of the Stylocellidae, the ornamentation of the distal cheliceral segment (character 4) can be found only near the base of the distal segment in certain *Stylocellus* (Fig. 3) and in *Miopsalis*. Alternatively, the ornamentation may cover a larger portion of the distal segment, as in *Fangensis leclerci* (Rambla 1994: Plate II, figure 1), or in certain *Stylocellus* (*S. silhavyi* and *S. gryllospecus*; Rambla 1991; Shear 1993b). The type species of the genus has not been examined, but according to Hansen & Sørensen (1904: Plate II, fig. 4b), it may belong to this type of chelicerae with the distal segment mostly ornamented.

6. *Dentition of the mobile digit of the chelicerae: uniform (0), two types of dentition (1)*: The dentition of the mobile digit of the chelicerae is uniform in most cyphophthalmids, but there are two distinct types of dentition in members of the Pettalidae (Juberthie 1970b: fig. 3) except in *Parapurcellia*.

7. *Basal article of chelicerae with dorsal crest: absent (0), present (1)*: A dorsal crest ("dorsal ridge" of Hansen & Sørensen (1904)) on the basal article of the chelicerae is present in most cyphophthalmids (e.g. Figs. 1–3), but not in those of the genus *Siro*, or in *Paramiopsalis*.

8. *Basal article of chelicerae with a ventral process: absent (0), present (1)*: A ventral protuberance on the basal cheliceral article ("processus basalis" of Hansen & Sørensen (1904)) is present in most cyphophthalmids (e.g. Figs. 1–3) but not in those lacking the dorsal crest, or in a few other sironids and pettalids.

9. *Basal article of chelicerae with a second ventral process: absent (0), present (1)*: Most cyphophthalmids have a ventral process on the basal cheliceral segment (character 9; Figs. 1, 2). Within the Stylocellidae, *Fangensis* and most members of the genus *Stylocellus* have a second ventral process ("processus inferior exterior" of Hansen & Sørensen (1904)), anterior to the typical ventral process and connected to the dorsal crest by an external keel (Fig. 3; see also Hansen & Sørensen 1904; Shear 1993b). This character is generally correlated with having the ornamentation

of the distal segment near the base (but not in *Fangensis*), while *Stylocellus silhavyi* lacks this second cheliceral ventral process. From the two species of *Miopsalis* examined here only one has the second ventral process and it is unknown whether the type species of the genus has it or not.

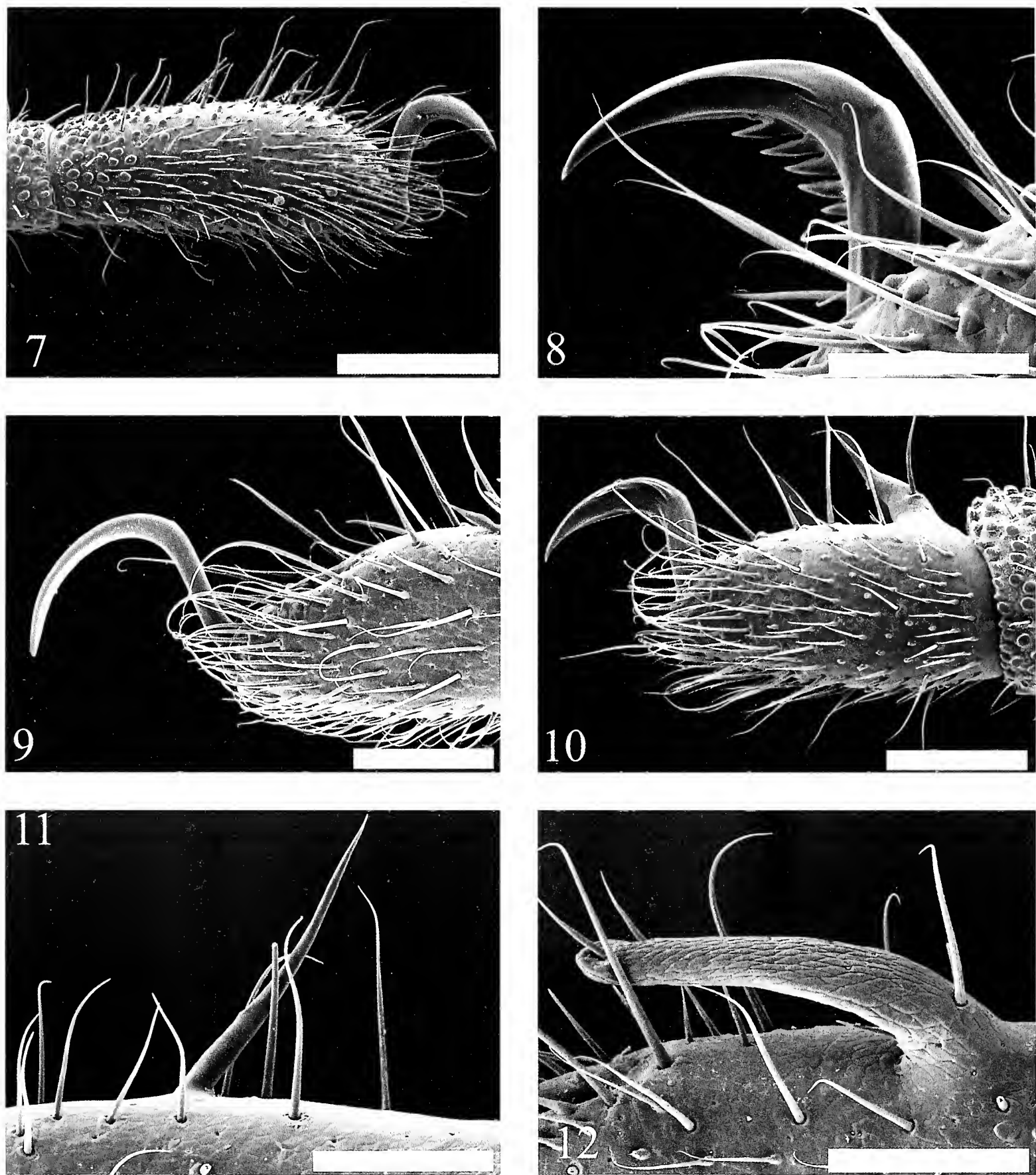
10. *Palpal trochanter with ventral process: absent (0), present (1)*: A ventral process in the palp trochanter (Juberthie 1970b: fig. 11) is found in pettalids from Australia, New Zealand, and South Africa, but not in *Chileogovea*. A similar structure is found in *Paramiopsalis ramulosus* (Juberthie 1962: fig. 10).

11. *Second coxa: free (0), fused to coxa of leg III (1)*: The coxa of leg II is free in members of the Sironidae and Pettalidae, while it is fused to the coxae of legs III and IV in members of the Stylocellidae (including *Fangensis* and *Miopsalis*), Neogoveidae (Fig. 4) and Ogoveidae. The genus *Troglosiro* has free coxa II, as well as "*Neogovea*" *mexasca* (Shear 1977) (Fig. 5). In contrast, *Paramiopsalis ramulosus* has the coxa II fused to the coxa of legs III and IV (Juberthie 1962), as does *Marwe coarctata*.

12. *Tarsus of leg I with a subapical modification where sensory hairs concentrate: absent (0), present (1)*: A subapical modification in tarsus of leg I (Fig. 6) is found in most cyphophthalmid species. The absence of such a process in "*Neogovea*" *mexasca* has been confirmed with the SEM, but the absence of such a structure in the sironids needs further study using SEM.

13. *Leg II ornamentation: metatarsus and tarsus smooth (0), metatarsus partially ornamented (1), metatarsus ornamented (2), ornamentation in the dorso-basal part of the tarsus (3), tarsus almost entirely ornamented (4)*: Juberthie (1970b) gave an account of different types of ornamentation in the legs I and II in several Temperophthalmi. Due to the observation of differences in ornamentation in legs I and II in certain cyphophthalmids, we prefer to restrict the definition of the character to the ornamentation of leg II, where the tarsus is not modified subapically as may occur with leg I.

14. *Claw of leg II with a row of ventral teeth: absent (0), present (1)*: While most cyphophthalmids have a smooth claw II (Fig. 7), a row of ventral teeth is characteristic of all the members of the genera *Neogovea*, *Huita-*



Figures 7–12.—7. Smooth tarsal claw II of *Chileogovea oedipus*; 8. Toothed tarsal claw II of *Metagovea philipi*; 9. Smooth tarsal claw II of “*Neogovea*” *mexasca*; 10. Male IV tarsus with posterior adenostyle of *Metagovea philipi*; 11. Adenostyle of “*Neogovea*” *mexasca*; 12. Adenostyle of *Paragovia sironoides*. Scale bars = 50 μ m (Fig. 8), 100 μ m (Figs. 9–12), 200 μ m (Fig. 7).

ca, *Metagovea* (Fig. 8), *Paragovia*, *Troglosiro*, and *Metasiro*. “*Neogovea*” *mexasca* lacks this type of teeth (Fig. 9). These teeth are not considered homologous to the lateral pegs of certain *Parasiro*.

15. Male tarsus IV: entire (0), bisegmented (1): Tarsus of leg IV of males bears an ad-

enostyle, and in *Suzukielus sauteri* and certain members of Pettalidae (*Austropurcellia*, *Neopurcellia*, *Purcellia*, *Speleosiro*, and *Parapurcellia*) is bisegmented (Juberthie 1970b: fig. 5b).

16. Adenostyle: lamelliform (0), with a tuft of setae (1), plumose (2): The adenostyle is

generally lamelliform (Figs. 10–12), but in Stylocellidae, *Metasiro* (Shear 1980: fig. 26) and all the species of *Neogovea* (except “*Neogovea*” *mexasca*: Fig. 11) the adenostyle terminates in a tuft of setae (Shear 1977, 1980). The adenostyle of *Paramiopsalis ramulosus* is plumose (Rambla & Fontarnau 1984: fig. 5).

17. *Adenostyle in the most-basal region of the tarsus: absent (0), present (1)*: The position of the adenostyle is highly variable, tending to be near the middle of the tarsus in members of the Stylocellidae. In members of the genera *Metagovea* (Fig. 10), *Huitaca*, *Paragovia* (Legg 1990: fig. 15), and *Metasiro* (Shear 1980: figure 26) the adenostyle emerges from the most-basal portion of the tarsus. However, *Paragovia sironoides* (Fig. 12) does not have an adenostyle at the most-basal region of the tarsus.

18. *Ovoid plate on male tarsus IV: absent (0), present (1)*: An ovoid plate on the internal-lateral side of the male tarsus IV was described for *Fangensis leclerci* (Rambla 1994: plate III, figs. 1, 2), and is also found in a new species of *Fangensis* from Thailand collected by P. Schwendinger.

19. *Male coxae IV meeting ventrally in the midline: absent (0), present (1)*: The coxae of leg IV generally meet in the midline in males (Fig. 13), but in certain species of the Ogoveidae and Neogoveidae, they form a tube-like structure for the penis, not meeting in the midline (Fig. 4).

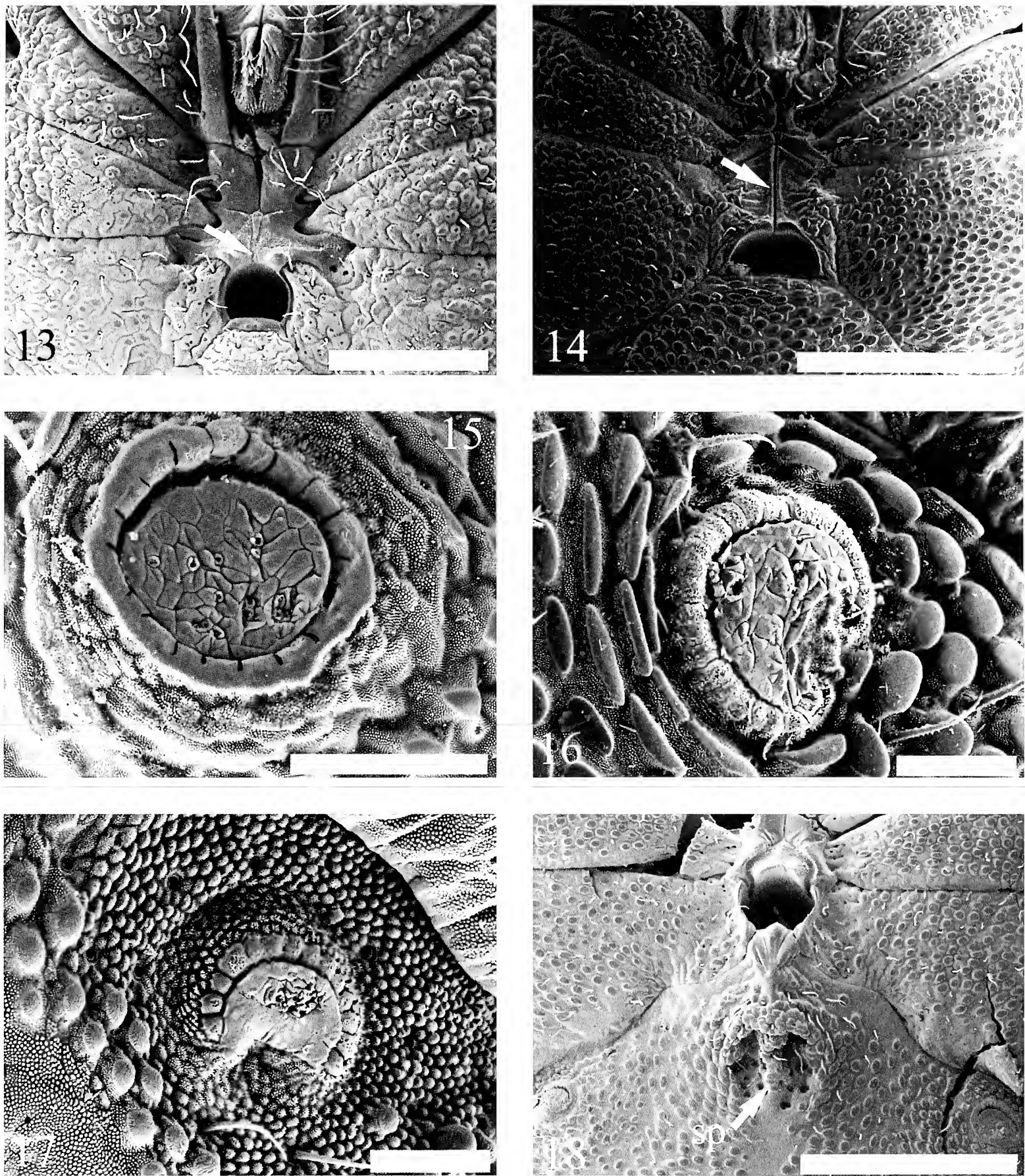
20. *Male gonostome small, with coxae IV meeting ventrally for a distance longer than the length of the genital opening: absent (0), present (1)*: In most members of the Pettaliidae, the male genital opening is very small, with the coxae IV meeting in the midline forming the solid anterior wall of the gonostome. In this case the gonostome is always shorter than the length of the coxae IV that run parallel in the midline (Fig. 14).

21. *Spiracle shape: circular (0), open circle (1), “C” shaped (2)*: Spiracle morphology has been overlooked in cyphophthalmid taxonomy, although it seems to be conserved at the familial level. Typical sironids, most neogoveids (including “*Neogovea*” *mexasca*, Fig. 15), *Ogovea*, *Troglosiro* and *Marwe* have circular spiracles. All pettalids, some neogoveids (*Neogovea microphaga* and two undescribed neogoveids from Trinidad and Venezuela), *Metasiro* and *Suzukielus* have spiracles that

are an open circle (e.g. *Chileogovea oedipus*, Fig. 16). All the stylocellids (including *Fangensis* and *Miopsalis*) have spiracles shaped like the letter “C” (Fig. 17). *Speleosiro argasiformis* bears a special type of spiracles, resembling the open circular type of typical pettalids, but it is so open that it resembles the “C” type of stylocellids. However, the direction of the aperture corresponds to that of the pettalids and not that of the stylocellids, and therefore we have coded *Speleosiro* as belonging to the open circle type.

22. *Male sternal glands: absent (0), present (1)*: Sternal secretory glands have been described for *Ogovea nasuta* and *Huitaca ventralis* (Fig. 18), and have been used to suggest a sister group relationship for these two genera (Shear 1979, 1980). Similar structures of possible secretory function have been recently found in *Metagovea philipi* (Figs. 19, 20), two undescribed *Metagovea* species from Ecuador, and *Paragovia sironoides* (Figs. 21, 22). Jubertie (1979) reported a type of secretory structures for the genus *Troglosiro* similar to the ones found in the Neogoveidae, although according to Shear (1980) these structures have questionable homology with those of *Ogovea* and *Huitaca* as they do not fulfill the criterion of positional homology. Here we have chosen to code the sternal glands of *Huitaca*, *Ogovea*, *Metagovea*, *Paragovia*, and *Troglosiro* as homologous structures.

We have examined the types and all the material reported in the literature of *Brasilogovea microphaga* (synonymized by Shear 1980), “?Gen.” *enigmaticus*, and all the species of the genus *Neogovea*. “*Neogovea*” *mexasca* clearly lacks the sternal glands when studied with an SEM. Unfortunately, the male of “?Gen.” *enigmaticus* is unknown, and from the other species, all the known males except one specimen of *N. immsi* lack the sternal area after having been dissected to study the penis. The single complete male of *N. immsi* has the ventral area covered by a film of an unidentified substance that cannot be removed from the specimen. This substance seems to emerge from some ventral gland and a few pores seem to be apparent in the centre of the second sternite. However, this needs confirmation with fresh material of males of *Neogovea*, and we have chosen to code it as a ‘?’. Therefore, with the exception of “*Neogovea*” *mexasca*, all members of *Neogovea* and related genera

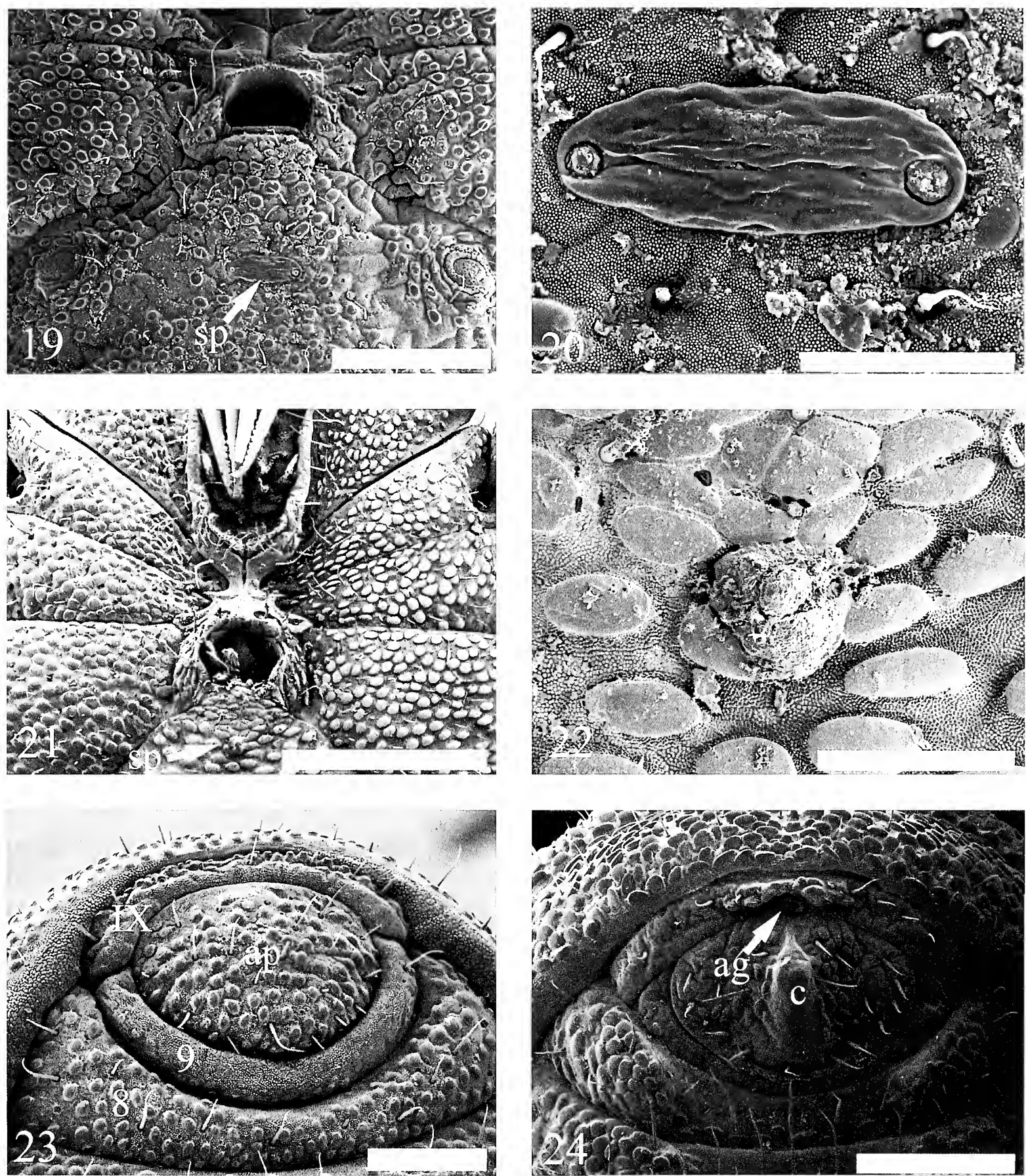


Figures 13–18.—13. Male ventral thoracic complex of and undescribed *Metagovea* species from Chiriboga (Ecuador) showing the short area of contact of the IV coxae; 14. Male ventral thoracic complex of *Chileogovea oedipus* showing the large contact area of the IV coxae; 15. Circular spiracle of “*Neogovea*” *mexasca*; 16. Open circular spiracle of *Chileogovea oedipus*; 17. Detail of the spiracular area of *Stylocellus ramblae* with the spiracle in the center; 18. Male sternal area of *Huitaca ventralis* showing the sternal pores (sp). Scale bars = 50 μ m (Figs. 15–17), 200 μ m (Fig. 13), 500 μ m (Figs. 14, 18).

are coded as ‘?’, although we believe that sternal organs may be found when fresh material is examined.

23. *Sternal apophysis of male*: absent (0),

present (1): A sternal apophysis in the ventral region is found in males of the genus *Ogovea* (e.g. Shear 1980: fig. 27) but not in any other cyphophthalmids.



Figures 19–24.—19. Male sternal area of *Metagovea philipi* showing the sternal pores (sp); 20. Detail of the sternal pores of *Metagovea philipi*; 21. Male sternal area of *Paragovia sironoides* showing the sternal pores (sp); 22. Detail of the sternal pores of *Paragovia sironoides*; 23. Female anal region of *Stylocellus ramblae* showing the anal plate (ap) and the unfused sternites 8, 9, and tergite IX; 24. Male anal region of *Chileogovea oedipus* showing the longitudinal carina of the anal plate (c), and the opening of the anal glands (ag). Scale bars = 50 μm (Figs. 20, 22), 100 μm (Fig. 23), 200 μm (Figs. 19, 24), 400 μm (Fig. 21).

24. Sternite 8, 9, and tergite IX: all free (0), sternites 8 and 9 fused (1), sternite 9 and tergite IX fused, but sternite 8 free (2), all fused into corona analis (3): The different degrees

of fusion of sternites 8 and 9, and tergite IX have been extensively discussed in the literature (Juberthie 1970b; Shear 1980). All segments are free in the Stylocellidae and in most

members of the Pettalidae, but not in *Pettalus cimiciformis*, in which sternite 9 is fused to tergite IX, but sternite 8 remains free. Sternites 8 and 9 may show different degrees of fusion leaving tergite IX free as in at least some *Parasiro* (only fused in the midpart) or in *Metasiro* and *Paramiopsalis* (almost completely fused), but until more detailed study of these conditions is conducted using SEM, we prefer not to separate these two states. *Ogovea*, *Troglosiro*, *Siro*, *Marwe*, and the Neogoveidae all have a complete corona analis (all segments fused).

25. *Relative position of sternite 9 and tergite IX: stylocellid type (0), pettalid type (1)*: In those Cyphophthalmi without a complete corona analis, the relative position of sternite 9 and tergite IX shows two typical configurations. A first configuration, here named "stylocellid type" is illustrated in Fig. 23, in which both sclerites meet towards the midline of the anal plate, and sternite 8 does not contact tergite IX. This is found in all stylocellids and those sironids without a complete corona analis. In *Suzukielus* and the females of all the pettalids (the males may have modified anal regions), a "pettalid" type occurs (e.g. Fig. 24), in which tergite IX covers laterally sternite 9, and clearly meets sternite 8.

26. *Male tergite IX: entire (0), divided (1)*: Tergite IX is divided in the males of *Suzukielus sauteri* and in several Pettalidae, such as certain species of *Austropurcellia*, *Neopurcellia*, *Rakaia*, and *Parapurcellia*.

27. *Male anal plate: without modifications (0), with longitudinal carina (1), with concentration of setae (2)*: Male anal plates are similar to those of females, without modifications in all the Tropicophthalmi and in some sironids, *Troglosiro*, *Pettalus*, and in some undescribed pettalids from Western Australia (here represented by the terminal 'Pember-ton'). Some members of the Sironidae (*Paramiopsalis*, *Siro*, and *Suzukielus*), and *Chileogovea* (Fig. 24) have a longitudinal carina. Finally, most members of the Pettalidae have anal plates extremely modified with all kinds of concentrations of setae such as tufts of setae in a groove in the anal operculum (e.g. *Purcellia*, *Parapurcellia*, *Speleosiro*), a "scopula" on the dorsal surface of the anal plate (e.g. *Rakaia*, *Neopurcellia*), or an "anterior scopula" (*Austropurcellia*).

28. *Male tergite VIII bilobed: absent (0),*

present (1): Tergite VIII becomes bilobed in the males of several pettalid species.

29. *Male abdominal exocrine glands (anal glands): absent (0), present (1)*: The presence of a special type of abdominal exocrine glands associated with the anal complex of males (Juberthie 1962, 1967) has been observed in several species of the families Sironidae and Pettalidae, and its function is probably for dispensing a pheromone (Shear 1980). Although the anal glands may be directly associated to some of the modifications of the anal plate and tergite IX, at least in the genus *Fangensis*, the anal glands do not entail other specific modifications. For this reason, we have coded this character independently. Anal glands have been specifically reported in *Fangensis leclerci* (Rambla 1994), *Paramiopsalis ramulosus* (Juberthie 1962), *Siro rubens* (Juberthie 1967), *Suzukielus sauteri* (Juberthie 1970a), and *Austropurcellia scoparia* (Juberthie 1988). Anal glands have also been observed in *Chileogovea oedipus* (Fig. 24), *Metasiro americanus*, *Siro duricorius*, *Siro exilis*, *Neopurcellia florensis*, *Rakaia arctica*, *Purcellia illustrans*, *Speleosiro argasiformis*, and in the new species of *Fangensis* from Thailand. However, the tufts of setae did not allow detailed examination of *Pettalus cimiciformis* or *Parapurcellia silvicola*, and have been coded as '?'. The undescribed pettalid from Pember-ton lacks anal glands.

30. *Ventral plate of penis hypertrophied: absent (0), present (1)*: The ventral plate of the penis is hypertrophied in members of the genus *Neogovea* (*N. immsi*, *N. kamakusa*, *N. kartabo*, and *N. microphaga*), thickened apically and dorsoventrally bifurcate (Martens 1969; Shear 1977, 1980).

31. *Ventral setae of penis: absent (0), present (1)*: Ventral setae are found in the penis of most cyphophthalmid, and certain lineages show a tendency towards reduction of the number of setae. Ventral setae are absent in *Paragovia sironoides* (Legg 1990: fig. 8), *Neogovea immsi*, and "*Neogovea*" *mexasca* (Shear 1980: fig. 5).

32. *Ovipositor with sense organs: absent (0), present (1)*: The ovipositor of *Parasiro* lacks the sense organs commonly found in the ovipositors of the Cyphophthalmi (Juberthie 1970b: fig. 12).

Molecular data.—The molecular data comprise twelve cyphophthalmid species be-

longing to five families (Stylocellidae, Neogoveidae, Troglosironidae, Pettalidae, and Sironidae) and ten genera (*Stylocellus*, *Fangensis*, *Paragovia*, *Troglosiro*, *Chileogovea*, *Purcellia*, *Parapurcellia*, *Siro*, *Parasiro*, and *Paramiopsalis*) (see Table 1). Outgroups representing the other three major lineages of Opiliones, Eupnoi, Dyspnoi, and Laniatores, have been employed to root the cyphophthalmid trees. Sequence data for the 18S rRNA and D3 region of the 28S rRNA loci have been obtained following standard protocols for DNA extraction and amplification for Opiliones (Giribet et al. 1999, 2002), and sequenced in an ABI PRISM® 3100 Genetic Analyzer following manufacturer protocols.

Phylogenetic analysis.—The phylogenetic analysis of the morphological data set has been executed with the parsimony-based computer program NONA v. 2.0 (Goloboff 1998), using a heuristic search strategy with 1000 random addition replicates using tbr (tree bisection-reconnection) branch swapping, and retaining up to 10 trees per replicate (hold10000;hold/10;mult*1000). The results of this first round of searches were submitted to tbr swapping without limiting the number of trees (max*). Bremer support (BS) values (Bremer 1988) and relative Bremer supports (RFD) (Goloboff & Farris 2001) were calculated with the computer program TNT (Goloboff et al. 2000) holding 10,000 trees. Bremer support generates absolute values of the degree to which a tree is suboptimal compared to another. A defect of that method is that it does not always take into account the relative amounts of evidence contradictory and favorable to the group. This problem is diminished if the support of the group is calculated as the ratio between the amounts of favorable and contradictory evidence, as proposed by Goloboff & Farris (2001). Potential advantages of the relative supports over normal Bremer support are that they vary between 0 and 1 and they provide an approximate measure of the amount of favorable/contradictory evidence (for example, if the RFD is 0.25, the amount of contradictory evidence is 75% the amount of favorable evidence, so it is equivalent to the conflict of 4 characters versus 3).

The molecular data have been analyzed following the direct optimization method (Wheeler 1996) as implemented in the computer program POY (Wheeler & Gladstein

2000). The analyses have been executed in a Linux parallel cluster of 11 nodes running pvm (Parallel Virtual Machine) at Harvard University (darwin.oeb.harvard.edu), each node consisting of two Pentium III processors at 1000 MHz, and 1 Gbyte of RAM. An analysis of multiple parameters (different insertion/deletion to change ratios, and transversion to transition ratios) was performed following a sensitivity analysis sensu Wheeler (1995). Basically, the two molecular partitions have been analyzed independently and in combination for nine combinations of parameters (gap:transversion:transition 111, 121, 141, 211, 221, 241, 411, 421, 441), choosing the parameter that minimizes overall incongruence when the partitions are analyzed in combination, following a normalized ILD metrics (Farris et al. 1995; Wheeler 1995) (Table 2). For more detailed explanations of the analyses refer to previous work by one of the authors (Edgecombe et al. 1999; Giribet et al. 2001, 2002).

RESULTS AND DISCUSSION

The search strategy implemented in NONA yielded trees of minimal length in 404 out of the 1000 replications performed. Six hundred minimum-tree length trees were found after swapping to completion the trees found on each replicate, at 83 steps (CI = 0.50; RI = 0.83). The strict consensus of the morphological trees (Fig. 25) can be rooted in three alternative positions, according to the molecular results obtained (see below). Basically, the root is placed between the Stylocellidae and the remaining taxa (rooting option 1), or between the Pettalidae and the remaining taxa (rooting option 2). Since molecular data are not available for *Suzukielus*, the root could also potentially be placed between *Suzukielus* and the sironids (rooting position 3).

The morphological trees (irrespective of where they are rooted) show the monophyly of Stylocellidae and Pettalidae, but the strict consensus of all the shortest trees shows irresolution for the Sironidae and Neogoveidae. The Stylocellidae clearly includes the genera *Fangensis* and *Miopsalis* (RFD = 100), a result also corroborated by the molecular data, which support monophyly of *Fangensis* and the two species of *Stylocellus* included for all parameter sets for the combined molecular (Figs. 26A & B), and 18S rRNA (Fig. 26C)

Table 1.—Opilionid taxa employed in the molecular analysis, country of origin, collector, and molecular partition represented.

Eupnoi: Phalangidae				
<i>Opilio parietinus</i>	Canada	R. Holmberg	18S rRNA	28S rRNA
Dyspnoi: Nipponopsalidae				
<i>Nipponopsalis abei</i>	Japan	N. Tsurusaki	18S rRNA	28S rRNA
Laniatores: Oncopodidae				
<i>Oncopus</i> cfr. <i>alticeps</i>	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
Cyphophthalmi				
Family Stylocellidae				
<i>Stylocellus</i> sp. BL	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
<i>Stylocellus</i> sp. JP	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
<i>Fangensis</i> sp.	Thailand	P. Schwendinger	18S rRNA	28S rRNA
Family Neogoveidae				
<i>Paragovia sironoides</i>	Equatorial Guinea	J. Lapuente & C. E. Prieto	18S rRNA	28S rRNA
Family Troglосironidae				
<i>Troglosiro</i> sp.	New Caledonia	G. B. Monteith	18S rRNA	28S rRNA
Family Pettalidae				
<i>Chileogovea oedipus</i>	Chile	J. Miller, F. Alvarez, J. Coddington	18S rRNA	
<i>Purcellia illustrans</i>	South Africa	G. Giribet & L. Prendini	18S rRNA	28S rRNA
<i>Parapurcellia silvicola</i>	South Africa	G. Giribet & L. Prendini	18S rRNA	28S rRNA
Family Sironidae				
<i>Parasiro coiffaiti</i>	Spain	E. Mateos	18S rRNA	28S rRNA
<i>Paramiopsalis ramulosus</i>	Spain	G. Giribet & M. K. Nishiguchi	18S rRNA	28S rRNA
<i>Siro rubens</i>	France	G. Giribet	18S rRNA	28S rRNA
<i>Siro valleorum</i>	Italy	Ferrario, Pantini, Pellizzoli, Valle	18S rRNA	28S rRNA

Table 2.—Tree length for the individual (18S: 18S rDNA; 28S: 28S rDNA) and combined (mol: molecular [18S + 28S]) datasets at different parameter values, and ILDs for the combined analyses. ILD number in bold reflects the minimum incongruence among data sets.

	18S	28S	MOL	ILD
111	308	175	497	0.0282
121	438	260	718	0.0279
141	690	422	1147	0.0305
211	325	198	537	0.0261
221	465	301	793	0.0340
241	741	503	1295	0.0394
411	350	232	607	0.0412
421	513	364	930	0.0570
441	837	628	1563	0.0627

analyses. This clade is clearly delimited biogeographically and is easily diagnosed by two unambiguous autapomorphies: an ornamented distal cheliceral segment (character 4), and “C”-shaped spiracles (character 21). Other characters showing some degree of homoplasy are the presence of eyes (character 1) and the presence of tarsi almost completely ornamented (character 13). The monophyly of the genus *Fangensis* is supported by the presence of ovoid plate in the male tarsus IV (character 18) and by the presence of anal glands in the male (character 29), a feature that placed them originally within the Sironidae (Rambla 1993), but is now known for members of the families Sironidae, Pettalidae and Stylocellidae, and hence a putative synapomorphy of the Cyphophthalmi lost in several lineages.

The families Neogoveidae, Ogoveidae, Troglosironidae, and the clade containing the Sironidae + Pettalidae form a polytomy in the strict consensus of the morphological analysis (Fig. 25). The 18S rRNA data (Fig. 26C) show a similar pattern, with monophyly of the non-stylocellids for all parameter sets, but with irresolution between *Parasiro*, Pettalidae, (*Siro* + *Paramiopsalis*), and (*Troglosiro* + *Paragovia*). However, certain parameters for the combined analysis of 18S rRNA + 28S rRNA show an alternative rooting position, with Pettalidae being the sister group of the remaining cyphophthalmids (Fig. 26A). Irrespective of the rooting option, all molecular data (all partitions and combination of partitions, as well as all parameter sets) show monophyly of (*Troglosiro* + *Paragovia*) (Fig.

26). A putative synapomorphy for Troglosironidae + Neogoveidae is the sternal glands in the males, although their presence needs to be confirmed in members of the genus *Neogovea* (see discussion of character 22). If this relationship of *Troglosiro* and Neogoveidae, a stable result based on molecular data, is confirmed by further data, the position of *Troglosiro* as the sister group of Sironidae + Pettalidae (Shear 1993a) could be discarded.

The genus *Ogovea* is monophyletic, although its relationships to other genera are ambiguous, and molecular data are not available. Its relationship with *Huitaca* previously suggested based on the sternal secretory organs (Shear 1979) is not supported in this analysis since the character appears to be more widely distributed than previously thought. Sternal secretory organs are present in all males of the genus *Metagovea* examined so far (Figs. 19, 20), as well as in *Paragovia* (Figs. 21, 22). The morphology of *Huitaca* is also similar to that of other undescribed species of *Neogovea* from Trinidad and Venezuela, sharing the same cheliceral type (character 3), and differs considerably from the genus *Ogovea*. Neogoveid genera (*Paragovia*, *Huitaca* and *Metagovea*), and the “true” *Neogovea* (*Neogovea*, *Brasilogovea*, “?Gen.”) are not resolved by the present morphological data, and they form a polytomy with Ogoveidae, Troglosironidae, and Sironidae—Pettalidae in the morphological tree. We will deal with these specific relationships in a forthcoming article revising the South American Neogoveidae.

The position of “*Neogovea*” *mexasca* is not consistent with previous classifications (Shear 1977, 1980). “*Neogovea*” *mexasca* clusters within the clade containing sironids and pettalids, due to many morphological characters. For example, coxae II are not fused to coxae III; the second leg claw lacks the ventral teeth (Fig. 9); and the chelicerae are elongated (Fig. 2) but with a large claw (not of the attenuate type typical of *Neogovea*). “Sironids” are here represented by two clades, one clade containing the genus *Parasiro*, and another clade containing the genera *Siro*, *Paramiopsalis* and *Marwe*, as sister group to *Suzukiellus* + Pettalidae. Most of the relationships suggested for the clade containing the sironids are based on ambiguous optimizations, and character conflict may be very important. The sister

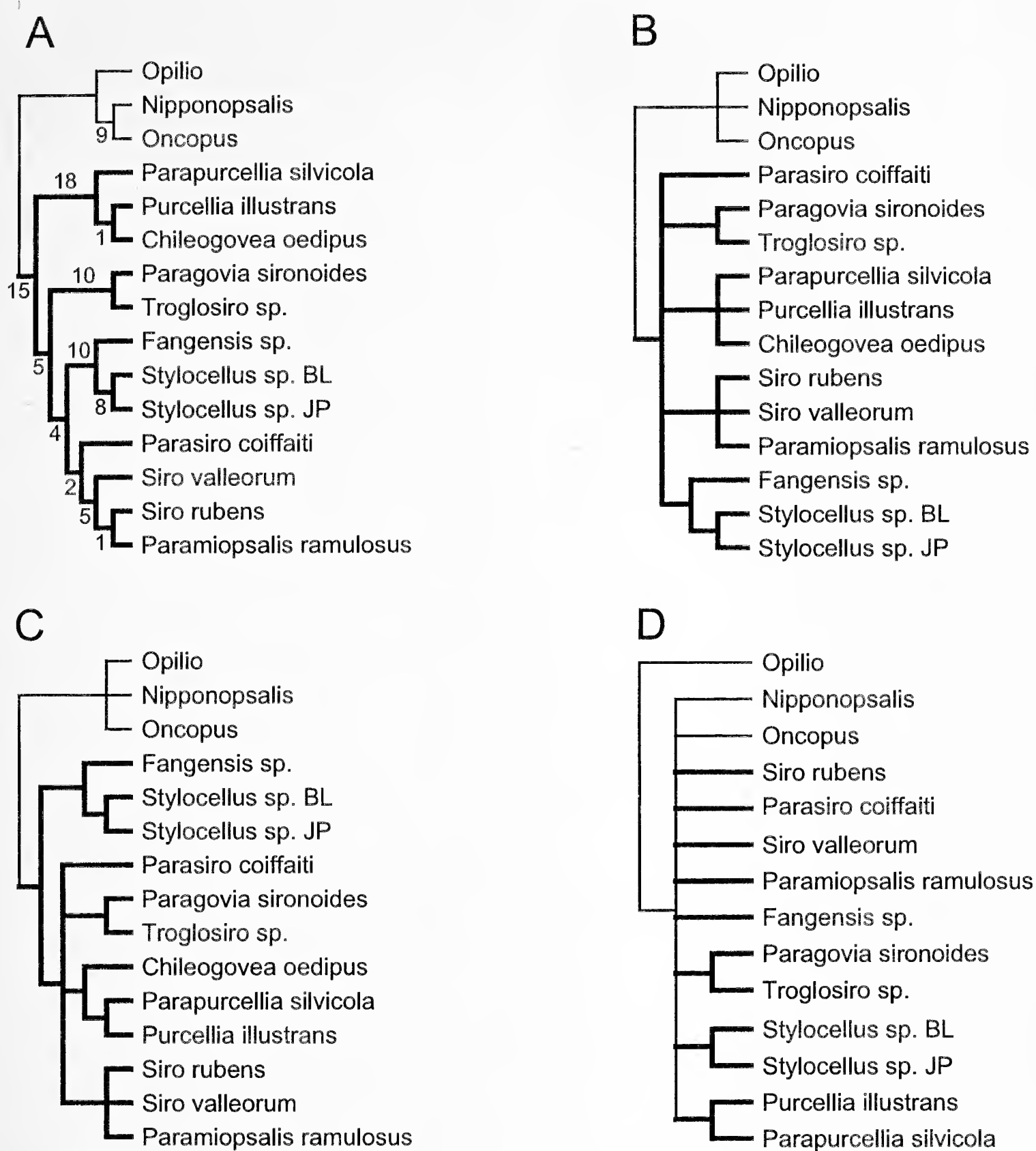


Figure 26.—Molecular trees with the cyphophthalmid taxa represented by thick branches. (A) Most parsimonious tree at gap cost = 2, transversion cost = transition cost = 1 (parameter set 211) for the combined analysis of 18S rRNA and 28S rRNA sequence data (537 steps; ILD = 0.0261). Numbers on branches represent absolute Bremer support values. (B) Strict consensus of all parameter sets examined (gap:transversion:transition 111, 121, 141, 211, 221, 241, 411, 421, 441) for the combined analysis of 18S rRNA and 28S rRNA sequence data. (C) Strict consensus of all parameter sets examined for the analysis of 18S rRNA sequence data. The split between Stylocellidae and the remaining cyphophthalmids is obtained for all parameter sets. (D) Strict consensus of all parameter sets examined for the analysis of 28S rRNA sequence data.

group relationship of *Marwe* and *Paramiopsalis* is based on the presence of fused second coxae, a character only shared by these two species within the “Sironidae”. We suspect that this relationship will not withstand future

analyses incorporating unknown penile and molecular characters of *Marwe*.
The position of *Metasiro* is uncertain, and more data are necessary to place this taxon unambiguously, although the claw of leg II

with a row of ventral teeth (character 14) or the basal position of the adenostyle (character 17) may indicate a relationship with Neogoveidae, while some trees place it as the sister group to Sironidae + Pettalidae (if rooting position 1 is used).

Pettalidae is a clear monophyletic group in both morphological (Fig. 25; RFD = 100; BS = 4) and molecular analyses for all partitions and parameter sets (Fig. 26A, BS = 18; Figs. 26B–D) with most of its members having dorsal ozophores (character 2), two types of dentition in the mobile digit of the chelicerae (character 6), and a small type of male gonostome (character 20). All pettalids also share with a few *Neogovea*, *Metasiro*, and *Suzukielus* an open circular type of spiracles (character 21). *Suzukielus sauteri* appears in fact to be the sister group to Pettalidae (or sister to the remaining Cyphophthalmi if rooting position 3 were correct), both taxa sharing the distinct relative position of tergite IX and sternites 8 and 9 (character 25). This character, together with the open circular spiracle only found in *Metasiro* among the classical sironids (all other sironids that we have examined have a circular spiracle) makes doubtful the phylogenetic position of *Suzukielus* as a true sironid as suggested by other authors.

Sironidae are in fact non-monophyletic irrespective of the rooting position selected. If the rooting position 1 were correct, then Sironidae would be paraphyletic with respect to Pettalidae, reflecting the idea of a “more complex phylogeny” of Sironidae–Pettalidae than that proposed by Shear (1980) (Juberthie 1989). Monophyly of *Siro* and *Paramiopsalis* is found in most molecular analyses for all parameters (Fig. 26), however, *Parasiro* does not cluster with the other sironids under certain parameter sets (Figs. 26B–C).

According to the molecular analyses, Cyphophthalmi are monophyletic (Fig. 26A–C), with the exception of certain parameter sets for the 28S rRNA partition (Fig. 26D), as shown in previous molecular analyses (Giribet & Wheeler 1999; Giribet et al. 1999, 2002), although two possibilities exist for rooting the morphological tree. One possibility suggests a root separating the Stylocellidae from the remaining cyphophthalmids (root 1 for all parameter sets for the 18S rRNA partition, and for parameter sets 111 and 241), or alternatively in the branch separating Pettalidae from

the remaining cyphophthalmids (root 2 or root 3 for parameter sets 111, 121, 211, 221, 411, 421, 441). These are the only two rooting possibilities suggested by the molecular analyses, and both are equally parsimonious under certain parameter sets (111, 241). These alternative rooting positions may have very different morphological and biogeographical implications. A split between the Pettalidae and the remaining cyphophthalmids, as suggested by most combined 18S rRNA + 28S rRNA trees would imply a split between Gondwanan and Laurasian cyphophthalmids, while an interesting morphological implication of the split between Stylocellidae and the remaining families (as suggested by 18S rRNA data alone) would have to do with the homology of the stylocellid eyes. With the data in hand, we cannot choose among either one of these two rooting positions. What seems clear at this point is that neither one of the two rooting alternatives is compatible with the classification of Hansen & Sørensen (1904) or Shear (1980), rooting between the Tropicophthalmi and the Temperophthalmi.

The molecular trees are highly congruent with the morphological analysis here presented, and recognize the monophyly of major families such as Stylocellidae, Pettalidae, and more ambiguously, Sironidae. These results are encouraging for pursuing further morphological and molecular research for internal cyphophthalmid phylogeny.

In general, the phylogenetic relationships here presented mainly agree with the classification system for the Cyphophthalmi proposed by Shear (1980), although alternative rooting positions would make Tropicophthalmi or Temperophthalmi paraphyletic. Both in Shear's and in the present analysis, the limitation in characters may result in weakly supported relationships. As an example, many nodes in the morphological tree here presented are unresolved for lack of information, or possess conflict of characters (low RFD). Only seven nodes have no conflicting characters (RFD = 100). From those, one supports the family Stylocellidae (*sensu* Giribet 2002), and another supports the family Pettalidae. However, the other families of Cyphophthalmi, Sironidae, Neogoveidae, and Ogoveidae (Troglosironidae is only represented by one species) *sensu* Shear (1980) are non-monophyletic. Hopefully, the addition of more char-

acters through the generalized use of SEM and DNA sequence data will help to refine our knowledge of the evolutionary history of this interesting arachnid group.

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Appendix 1.—Morphological data matrix.

Species	Characters
	000000000111111111222222222333 12345678901234567890123456789012
<i>Stylocellus beccarii</i>	1101001110114001001020000000001?
<i>Stylocellus javanus</i>	11010011101140??00??2??00???????
<i>Stylocellus modestus</i>	110100111011400?00??2?000000????
<i>Stylocellus ramblae</i>	11010011101140010010200000000???
<i>Stylocellus sedgwicki</i>	110100111011400?00?020000000?01?
<i>Stylocellus silhavyi</i>	11011011001140010010200000000011
<i>Fangensis leclerci</i>	01011011101140010110200000?01011
<i>Fangensis</i> sp.	?1011011101140010110200000101???
<i>Miopsalis</i> sp. 1	01010011001140?????2??00???????
<i>Miopsalis</i> sp. 2	01010011101140010?102?000000????
<i>Metasiro americanus</i>	0100-011000121011010100100001011
<i>Troglosiro juberthiei</i>	0100-0110001210000100103-0000011
<i>Paramiopsalis ramulosus</i>	0100-000-11000020010?00100101??1
<i>Parasiro coiffaiti</i>	0000-010-00010000010000100000010
<i>Parasiro minor</i>	0000-011000010000010000100000010
<i>Siro duricorius</i>	0100-000-000000000100003-0101011
<i>Siro exilis</i>	0100-000-000000000100003-010101?
<i>Siro rubens</i>	0100-000-000000000100003-0101011
<i>Siro valleorum</i>	0100-000-000000000100003-01010??
<i>Suzukielus sauteri</i>	0100-0110000001000101000111010?1
<i>Pettalus cimiciformis</i>	0210-1110001300000111002-001????
<i>Chileogovea oedipus</i>	0200-111000130000011100010101011
<i>Austropurcellia scoparia</i>	0100-110-10120100011100011211011
<i>Neopurcellia florensis</i>	0200-111010120100011100011211???
<i>Rakaia arctica</i>	0200-111010110000011100011211??1
<i>Pettalidae</i> sp., Pemberton	0200-111010110000011100010000???
<i>Parapurcellia silvicola</i>	0100-010-1011010001110001121????
<i>Purcellia illustrans</i>	0200-111010110100011100010211011
<i>Speleosiro argasiformis</i>	0200-111010110100010100010211011
<i>Ogovea nasuta</i>	0100-0110011400000000113-000001?
<i>Ogovea</i> sp.	0100-0110011400000000113-0000???
<i>Paragovia sironoides</i>	0100-0110011410000?00103-000000?
<i>Huitaca ventralis</i>	0110-0110011210010000103-000001?
<i>Metagovea disparunguis</i>	0100-0110011?1001000??03-0000???
<i>Metagovea oviformis</i>	0100-01100112?0010100?03-0000011
<i>Metagovea philipi</i>	0100-0110011210010000103-0000??1
<i>Neogovea immsi</i>	0110-0110011210100000?03-000010?
<i>Neogovea kamakusa</i>	0110-0110011210100000?03-00001??
<i>Neogovea kartabo</i>	0110-0110011410100?00?03-00001?1
<i>Neogovea microphaga</i>	0110-0110011410100101?03-000011?
?Gen. enigmaticus	0110-011001141?????0??3-??????1
<i>Neogovea mexasca</i>	0100-0110000200000100003-0000001
<i>Marwe coarctata</i>	0000-000-01050000?100?03-000????

Appendix 2.—List of species studied indicating if males (♂) and/or females (♀) have been examined, and depository institutions of the studied material.

-
- Stylocellus beccarii* (Thorell 1882) (♂ & ♀, ZMB, ZMUC)
Stylocellus javanus (Thorell 1882) (♀, AMNH)
Stylocellus modestus Hansen & Sørensen 1904 (♀, ZMUC)
Stylocellus ramblae Giribet 2002 (♂ & ♀, FMAC, MCZ, WAM)
Stylocellus sedgwicki Shear 1979 (♀, MCZ)
Stylocellus silhavyi Rambla 1991 (♂ & ♀, CCol)
Fangensis leclerci Rambla 1994 (Material not examined)
Fangensis sp. (♂ & ♀, MHNG)
Miopsalis sp. 1 (♀, BMNH)
Miopsalis sp. 2 (♂, FMAC)
Metasiro americanus (Davis 1933) (♂ & ♀, AMNH, FMAC)
Troglosiro juberthiei Shear 1993 (♂ & ♀, AMNH)
Paramiopsalis ramulosus Juberthie 1962 (♂ & ♀, MCZ)
Parasiro coiffaiti Juberthie 1956 (♂ & ♀, MCZ)
Parasiro minor Juberthie 1958 (♂ & ♀, MHNG)
Siro duricorius (Joseph 1868) (♂ & ♀, CCol, MCZ, ZMB)
Siro exilis Hoffman 1963 (♂ & ♀, AMNH, FMAC, SMF)
Siro rubens Latreille 1804 (♂ & ♀, ZMB)
Siro valleorum Chemini 1989 (♂ & ♀, MCZ)
Suzukielus sauteri (Roewer 1916) (♂ & ♀, CCol, MHNG, SMF, ZMB)
Pettalus cimiciformis (Cambridge 1875) (♂, BMNH)
Chileogovea oedipus Roewer 1961 (♂ & ♀, AMNH, FMAC, MCZ)
Austropurcellia scoparia Juberthie 1988 (♂, & ♀, ANIC)
Neopurcellia florensis Forster 1948 (♂ & ♀, NMSA)
Rakaia arctica Cantrell 1980 (♂ & ♀, ANIC)
Pettalidae sp. from Pemberton, Western Australia (♂ & ♀, FMAC)
Parapurcellia silvicola (Lawrence 1939) (♂ & ♀, MCZ, SAM, NMSA)
Purcellia illustrans Hansen & Sørensen 1904 (♂ & ♀, MCZ, SAM, NMSA, ZMUC)
Speleosiro argasiformis Lawrence 1931 (♂ & ♀, SAM, NMSA)
Ogovea nasuta (Hansen 1921) (♂, ZMUC)
Ogovea sp. from Abong Mbang, Cameroon (♂ & ♀, BMNH)
Paragovia sironoides Hansen 1921 (♂ & ♀, C. Prieto, leg., MCZ)
Huitaca ventralis Shear 1979 (♂, MCZ)
Metagovea disparunguis Rosas Costa 1950 (Material not examined)
Metagovea oviformis Martens 1969 (♂ & ♀, SMF)
Metagovea philipi Goodnight & Goodnight 1980 (♂ & ♀, AMNH)
Neogovea immsi Hinton 1938 (♂ & ♀, BMNH)
Neogovea kamakusa Shear 1977 (♂, AMNH)
Neogovea kartabo (Davis 1937) (♂ & ♀, AMNH)
Neogovea mexasca Shear 1977 (♂ & ♀, AMNH)
Neogovea microphaga (Martens 1969) (♂, SMF)
?Gen. *enigmaticus* Martens 1969 (♀, SMF)
Marwe coarctata Shear 1985 (♀, AMNH)
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THE AFRICAN SPIDER GENUS *SINGAFROTYPA* (ARANEAE, ARANEIDAE)

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ABSTRACT. The African spider genus *Singafrotypa* Benoit is redescribed and transferred from the tetragnathid subfamily Nephilinae to the araneid subfamily Araneinae. Cladistic analysis of the matrix of Scharff & Coddington (1997) with the addition of two *Singafrotypa* species supports this new placement. *Singafrotypa acanthopus* Simon, the type species of the genus, is described along with two new species: *Singafrotypa okavango* new species from Botswana, and *Singafrotypa mandela* new species from South Africa. *Singafrotypa goliath* Benoit is transferred to *Neoscona* Simon (Araneidae, Araneinae).

Keywords: Araneae, *Singafrotypa*, *Neoscona*, Araneidae, Araneinae, Nephilinae, Tetragnathidae, cladistics, Africa

The subfamily Nephilinae was first formally recognized by Simon (1894), although its familial placement within Araneoidea has changed repeatedly (see Hormiga et al. 1995 for history of placements), until recently placed within Tetragnathidae (Levi 1986; Levi & von Eickstedt 1989; Coddington 1990). Nephilinae as currently delimited contains eight genera with 55 species and 28 subspecies (Platnick 2000).

Hormiga et al. (1995) studied the higher level phylogenetics of Tetragnathidae and found that nephilines (represented in their matrix by five genera) were monophyletic and sister to the remaining tetragnathids. However, the status of the “nephiline” genera *Deliochus* Simon 1894 (from Australia), *Singafrotypa* Benoit 1962 (from Africa) and *Perilla* Thorell 1895 (from Myanmar and Vietnam), has remained untested. These genera are currently placed in Tetragnathidae (Platnick 1997, 2000). Until now no *Singafrotypa* males have been described, which has made its placement difficult. In this paper we redescribe *Singafrotypa acanthopus* (Simon 1907), the type species, describe two new species from southern Africa, and test the familial placement of *Singafrotypa* using quantitative cladistic methods. The results suggest that *Singafrotypa* is an araneid, not a tetragnathid.

Taxonomic history.—Simon (1907) described *Singotypa acanthopus* from the western African island of Fernando Poo (today Bioko of Equatorial Guinea). Simon (1894) previously designated *Epeira melania* L. Koch 1871 as the type species of his genus *Singotypa* Simon 1894 (later synonymized with *Phonognatha* by Dondale (1966)). Simon (1894) placed *Singotypa* in the group Phonognatheae within the subfamily Nephilinae of his family Argiopidae, today’s Araneoidea (Simon’s Argiopidae included many families recognized today). *Singotypa acanthopus* was the first species described from Africa in this otherwise Australian genus.

Lessert (1930) recorded a female of *Singotypa acanthopus* from Poko, Congo (now the Democratic Republic of Congo). Lessert (1930) apparently examined one of Simon’s original specimens from MCSNG, which he referred to as the type, as he stated that the type female is smaller than the one examined from Congo. Lessert (1930) also published a drawing of the epigynum with a redescription of the species, at the time known from two African localities.

In 1962 Benoit erected *Singafrotypa*, a new monotypic genus containing only *Singotypa acanthopus*. Benoit based his redescription of *Singafrotypa acanthopus* on one of Simon’s

original females deposited in MCSNG, which he referred to as the holotype, and retained the genus in the araneid subfamily Nephilinae (Benoit 1962). Later, Benoit (1963) described the second species of the genus, *Singafrotypa goliath* Benoit 1963 from a single female from Ivory Coast. Unfortunately, the holotype of *S. goliath* is lost (R. Jocqué, *in litt.*). However, Benoit's illustrated description is sufficient to transfer the species to the araneid genus *Neoscona* Simon 1864 (see below).

METHODS

General methods of study are described in Hormiga (1994). All morphological observations and illustrations were made using a Leica MZ APO dissecting microscope. Illustrations were made using a camera lucida and rendered on coquille board. Measurements were made using a reticle and are in millimeters. Abbreviations of the specimen repositories are explained in the Acknowledgments.

Cladistic analysis.—Upon examining the first available males of *Singafrotypa acanthopus* (the type species of the genus) and *S. okavango* new species, it becomes clear that the placement of the genus within Tetragnathidae is not justified. The presence of male araneid characters such as a radix, median apophysis, a pair of male palpal patellar setae, and male coxal hook, suggests *Singafrotypa* is an araneid. These features along with the female epigynal scape are absent in tetragnathids. To cladistically test the genus' araneid placement, we used the published matrix of Scharff & Coddington (1997), which has 57 araneid genera plus 13 genera from eight outgroup families including Tetragnathidae scored for 82 morphological and behavioral characters. To this character matrix we added *S. acanthopus* and *S. okavango*. Thus the matrix we analyzed had a total of 72 taxa scored for 82 characters. The *Singafrotypa* lines of the matrix are given in Table 1.

The parsimony analyses were performed using the computer programs NONA version 2.0 (Goloboff 1993) and PAUP* version 4.0b4a (Swofford 2000). In NONA we used

search parameters hold 10000, mult*500 and max under both 'amb -' and 'amb ='. In PAUP we used random taxon addition for 10 replicates and TBR branch swapping. Winclada version 0.9.99m24 (Nixon 2000) was used to display and manipulate trees and matrices for NONA. The 14 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971). Ambiguous character optimizations were usually resolved so as to favor reversal or secondary loss over convergence (Farris optimization or ACCTRAN).

RESULTS

Heuristic searches in NONA, under "amb-" produced 748 most parsimonious trees of 287 steps, with consistency and retention indices of 0.34 and 0.74, respectively; allowing for more ambiguous support ("amb=") results in 1464 trees of the same length. The parsimony heuristic searches in PAUP* produced 2005 trees of minimal length (287 steps), with consistency and retention indices of 0.34 and 0.75, respectively. When these trees are filtered to remove topologies with polytomies for which more resolved trees exist, the number of cladograms is reduced to 406. The strict consensus of these two subsets of trees is, of course, identical. Successive character weighting (Farris 1969) in PAUP using a base weight of 100 and the maximum value of the rescaled consistency index produces stable results after the fourth iteration (215 trees of 296 steps under equal weights).

All the minimal length topologies, including those from successive character weighting, have in common the placement of *Singafrotypa* within the araneid subfamily Araneinae, as well as the monophyly of Araneidae and Tetragnathidae. These results are topologically congruent with those of Scharff & Coddington (1997).

In the strict consensus cladogram of the 2005 trees found by PAUP much resolution within Araneinae is lost, but the following cladistic structure is retained: *Scoloderus* (*Acanthepeira* plus the rest of Araneinae, including

Table 1.—Coding of morphological and behavioral characters of Scharff & Coddington (1997) for *Singafrotypa acanthopus* and *S. okavango* new species.

<i>S. acanthopus</i>	001111000000000110010100000101101100001100201000111??000-0000001000100210?????????
<i>S. okavango</i>	00111100000000011001010000010110110000110020110011100000-00000010001002?0?????????

Singafrotypa). This large clade of araneines, sister to *Acanthepeira*, is largely unresolved although it contains a clade which places monophyletic *Singafrotypa* as sister to *Aran-iella* (*Alpaida* (*Enacrosoma* + *Bertrana*)). In the strict consensus cladogram of the 1464 trees found under “amb=” in NONA, *Singafrotypa* falls into a large polytomy within the large araneine clade sister to *Acanthepeira*, but retains monophyly of both *Singafrotypa* species.

Singafrotypa acanthopus lacks the three synapomorphies currently hypothesized to support tetragnathid monophyly (Hormiga et al. 1995): absence (loss) of median apophysis, embolus and conductor spiraling with each other, and apical tegular sclerites. In *Singafrotypa*, as in other araneids, the median apophysis is present, the conductor and embolus do not spiral with each other and the tegular sclerites are not apical. *Singafrotypa acanthopus* has grooves in the booklung covers, an additional tetragnathid synapomorphy suggested by Scharff & Coddington (1997), but this character is homoplastic (see later). On the other hand, *S. acanthopus* has the following araneid synapomorphies: mesal orientation of the male palpal cymbium, presence of a radix, and the wide separation of lateral and median eyes. The presence of a sustentaculum on the fourth tarsi and grooved booklungs, both present in *S. acanthopus*, are synapomorphies of the clade containing all araneid subfamilies but excluding the genus *Chorizopes*. The presence of a tubercle on the male palpal femur and the presence of an epigynal scape, both synapomorphies of the subfamily Araneinae (Scharff & Coddington 1997), are present in *S. acanthopus*, and support the placement of *Singafrotypa* within the Araneinae.

DISCUSSION

This cladistic analysis suggests placement of *Singafrotypa* within the araneid subfamily Araneinae. The sample of tetragnathid and araneid genera in the matrix permitted *Singafrotypa* to join either family, but all most parsimonious trees place it within Araneidae. Our results should not be interpreted as a new proposal of relationships among the Araneinae. Neither Scharff & Coddington's (1997) study nor our own analysis involved studying African araneid genera hypothesized to be the

closest relatives of *Singafrotypa*, like some taxa of the “*Larinia* genus-group” revised by Grasshoff (1970a-c, 1971). Scharff & Coddington (1997: 357) designed their study to reconstruct the basic phylogenetic structure of Araneidae by detecting major lineages and their interrelationships and were mostly concerned with resolving relationships among genera of Gasteracanthinae and the whole “argiopoid clade” rather than the relationships within Araneinae.

Which genera, then, might be close relatives of *Singafrotypa*? Several features are shared between *Singafrotypa* and some other African araneid genera (see the *Singafrotypa* diagnosis below). However, in the absence of a more detailed phylogenetic context for the higher level relationships of araneids it is not possible to assess whether these shared features are plesiomorphic or apomorphic, and thus the question about the close relatives of *Singafrotypa* has to remain unanswered until we have a better understanding of the cladistic structure of Araneidae.

TAXONOMY

Family Araneidae Simon 1895

Genus *Singafrotypa* Benoit 1962

Singafrotypa Benoit 1962: 218; Brignoli 1983: 242; Platnick 1989: 299; Platnick 1993: 380; Platnick 1997: 452; Dippenaar-Schoeman & Jocqué 1997: 292. Type species, by original designation, *Singotypa acanthopus* Simon 1907.

Etymology.—The original generic name *Singotypa* Simon supposedly came from the resemblance to the cylindrical, posteriorly rounded, abdomen of the European araneid genus *Singa* C. L. Koch 1836 (cf. Simon 1894: 747). Benoit (1962) apparently conveyed the African origin of the spiders by modifying the name to *Singafrotypa*.

Diagnosis.—The genital morphology of *Singafrotypa* is similar to that of *Araneus* Clerck 1757 and *Larinia* Simon 1874. *Singafrotypa* differs from *Araneus*, *Larinia* and *Neoscona* by having a wide cephalic region in both sexes. In contrast, the *Araneus* male head region is always narrower than in females (Levi 1991). *Singafrotypa* has an elongated abdomen with parallel sides which overhang the spinnerets, unlike that found in *Araneus*. The scape of *Singafrotypa* is annulated, unlike in *Neoscona*. While *Larinia* can have an elon-

gate, oval abdomen, sometimes projecting behind and above the spinnerets (Harrod et al. 1990) as in *Singafrotypa*, *Singafrotypa* males have a hook on the first coxae, which is absent in *Larinia*. In *Singafrotypa* the second tibia is as thick as the first, while in *Larinia* it is thicker (Harrod et al. 1990). African *Larinia* were split into several genera by Grasshoff (1970b, c, 1971); all these genera, except *Paralarinia* Grasshoff, differ from *Singafrotypa* in somatic morphology. While the female abdomen and the epigynum of *S. acanthopus* resemble those of *Paralarinia incerta*, *Singafrotypa* differs from *Paralarinia* in the details of the palpal sclerites (cf. Grasshoff 1970c, fig. 20): relative position of subterminal and terminal apophyses, *Singafrotypa* conductor with marginal denticles and the median apophysis being denticulated.

Description.—Somatic morphology of the three known species is uniform and is illustrated for *S. acanthopus* (Figs. 1–3). Sexual dimorphism is not pronounced. Both sexes have an elongated body with stout spiny legs (Figs. 1–3), a dark brown prosoma with a wide cephalic region and widely separated median and lateral eyes (Figs. 2–3), a longer than wide sternum. Abdomen elongated and cylindrical, longer than wide, and caudally overhanging the spinnerets (Fig. 1, especially pronounced in females). While size, as well as shades of gray and brown coloration, vary within and among species, the general dorsum pattern is as illustrated in Figs. 2–3.

Males: Total length 7.49–9.0. Cephalothorax 3.47–3.78 long, 2.35–2.38 wide, 0.75–1.08 high. Sternum 1.56–1.64 long, 0.97–1.0 wide. Abdomen 4.26–5.7 long, 2.28–2.5 wide. First femur 2.82–3.13 long. Chelicerae with 5–6 prolateral and 3–4 retrolateral teeth, and 12–15 denticles in between. Pedipalp as in Figs. 4–5, 9–10.

Females: Total length 9.05–14.57. Cephalothorax 3.78–5.05 long, 2.28–3.14 wide, 1.13–1.6 high. Sternum 1.56–2.25 long, 1.06–1.36 wide. Abdomen 6.2–10.23 long, 2.64–4.9 wide. First femur 2.5–4.1 long. Chelicerae with 4–6 prolateral and 3–4 retrolateral teeth, and 15–30 denticles in between. Epigynum as in Figs. 6–8, 11–14.

Natural history.—Unknown. *Singafrotypa* cylindrical body with advanced spinnerets might suggest utilization of rolled leaves or grass stems as a retreat on the web, not unlike

the behavior of the Australian *Phonognatha* (Thirunavukarasu et al. 1996), or Asian *Perrilla* Thorell (Murphy & Murphy 2000, Kuntner in prep.). Three of four examined females of *S. okavango* had broken-off emboli stuck in the epigynal copulatory openings (Figs. 11–12).

Composition.—The genus comprises three species, two of which are new.

Distribution.—Western, central, and southern Africa.

Singafrotypa acanthopus (Simon 1907)

Figs. 1–8, 15

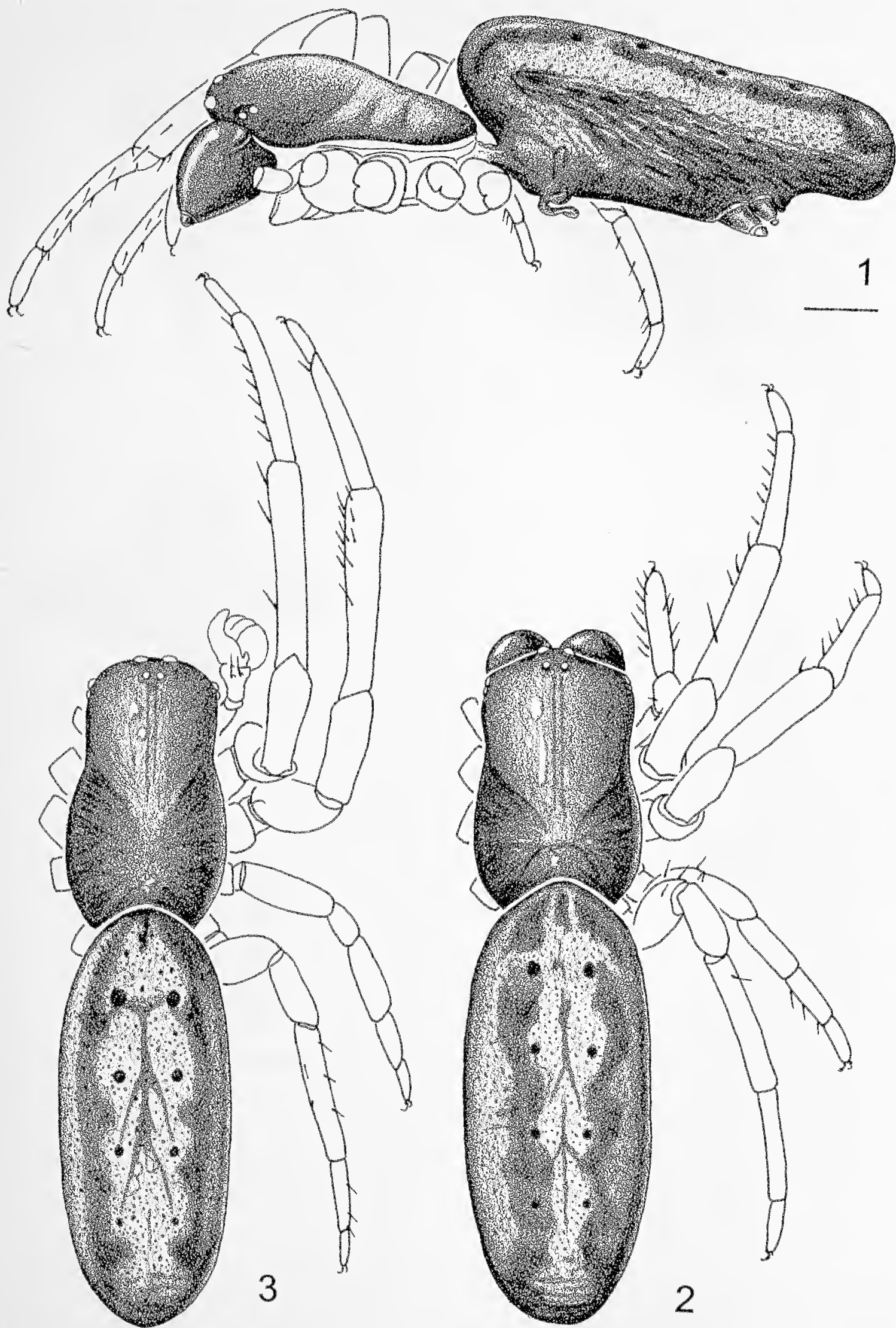
Singotypa acanthopus Simon 1907: 281–282, female, lectotype from Fernando Poo (designated herein), in MCSNG, examined; Lessert 1930: 626–627, fig. 9, female; Roewer 1942: 934; Bonnet 1958: 4060.

Singafrotypa acanthopus (Simon): Benoit 1962: 219–220, female; Brignoli 1983: 242; Platnick 1993: 380.

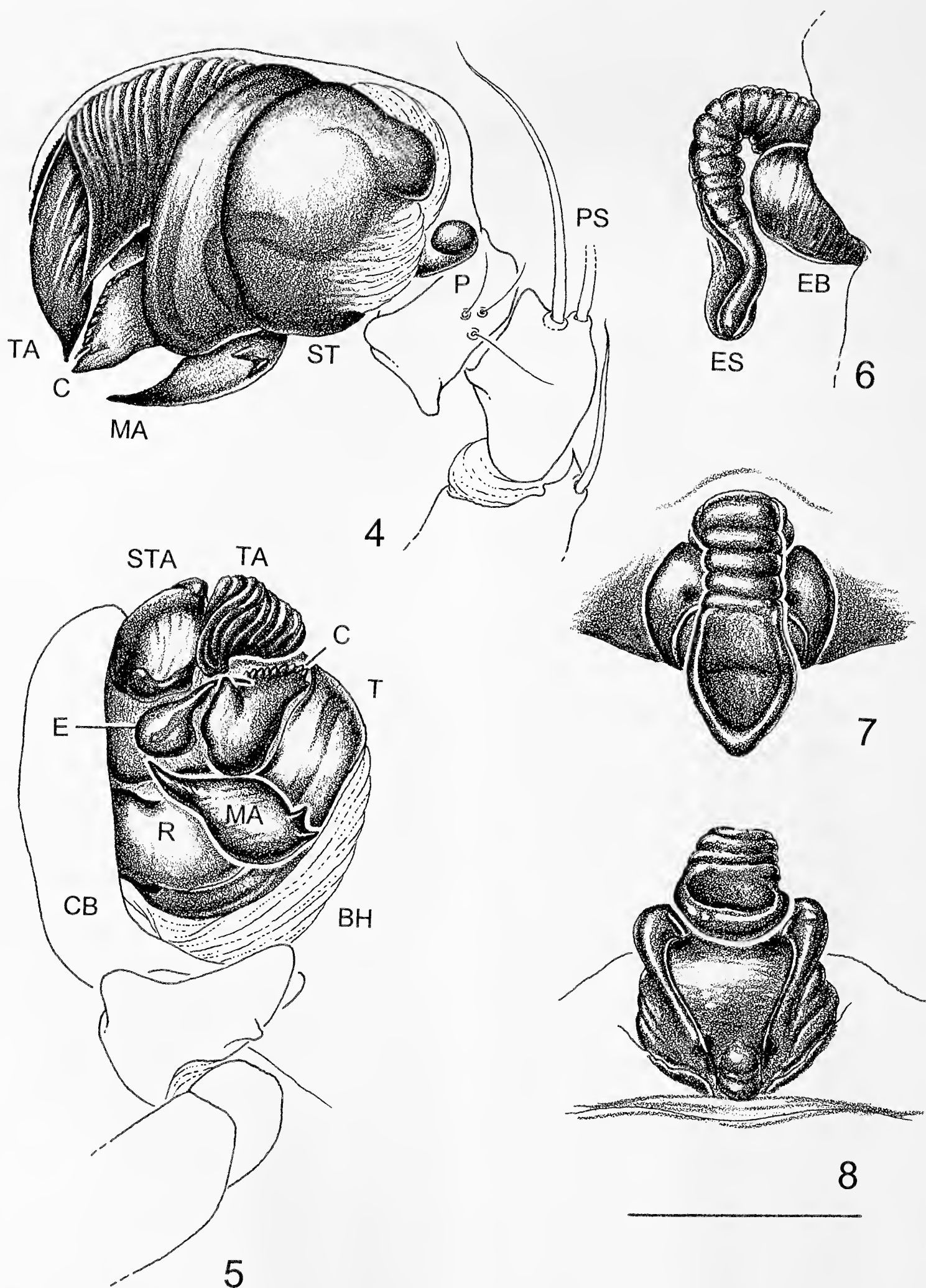
Types.—Simon (1907) described *Singotypa acanthopus* from specimens from Fernando Poo but did not designate a holotype, nor did he state how many females he examined in his type series. Since in his original description Simon reported the range of 8–9 mm as the total female length, we believe his type series included more than one female. Lessert (1930) and Benoit (1962) referred to the single female from MCSNG as the type and holotype, respectively. Since the existence of more than one female from Simon's type series is possible, we here fix the syntype female examined as the lectotype to become the unique bearer of the name *S. acanthopus*.

Note.—In his description of *Singafrotypa goliath*, Benoit (1963: 31, 32) erroneously referred to the name of the other species of *Singafrotypa* as "*S. clathrata* Simon". The error stems from Benoit confusing two of Simon's type specimens from MCSNG, *Singotypa acanthopus* Simon and *Clitaetra clathrata* Simon 1907. The species Benoit (1963: 31, 32) was referring to as "*S. clathrata* Simon", of course, is *S. acanthopus* Simon.

Diagnosis.—The males of *S. acanthopus* can be distinguished from those of *S. okavango* by the (Figs. 4–5) distal end of the terminal apophysis being shorter and not curved, larger embolus resting on conductor notch, conductor with marginal teeth pointing apically (mesally in *S. okavango*).



Figures 1–3.—*Singafrotypa acanthopus* (Simon 1907). 1–2. Female lectotype from Bioko, Equatorial Guinea; 1. Lateral; 2. Dorsal; 3. Male from Lamto, Ivory Coast, dorsal. Scale bar = 1.0 mm.



Figures 4–8.—*Singafrotypia acanthopus* (Simon 1907). 4–5. Left male palpus (Lamto, Ivory Coast); 4. Ectal; 5. Mesal; 6–8. Epigynum (lectotype); 6. Lateral; 7. Ventral; 8. Caudal. Scale bar = 0.5 mm. Abbreviations: BH = basal hematodocha; C = conductor; CB = cymbium; E = embolus; EB = epigynal base; ES = epigynal scape; MA = median apophysis; P = paracymbium; PS = palpal patellar setae; R = radix; STA = subterminal apophysis; ST = subtegulum; T = tegulum; TA = terminal apophysis.

Singafrotya acanthopus females can be distinguished from *S. mandela* by the absence of stout macrosetae on palpal tarsus, and the absence of stout short macrosetae laterally on paturon, both present in the latter species. *Singafrotya acanthopus* differs from both *S. okavango* and *S. mandela* by the epigynum shape (Figs. 6–8); epigynum base not heart-shaped (as it is in *S. okavango*), copulatory openings (ventral view) in the middle part of the epigynum base unlike in both other species. Scape with many wrinkles (fewer in *S. mandela*).

Description.—*Male* (from Lamto, Ivory Coast, Figs. 3–5). Total length 9.0. Cephalothorax 3.78 long, 2.35 wide, 1.08 high. Sternum 1.64 long, 1.0 wide. Abdomen 5.7 long, 2.5 wide. First femur 2.82 long. Chelicerae with 6 prolateral and 3 and 4 retrolateral teeth, and approximately 15 denticles in between. Pedipalp as in Figs. 4–5.

Female (lectotype): (Figs. 1–2, 6–8, 15): Total length 9.05. Cephalothorax 3.78 long, 2.28 wide, 1.19 high. Sternum 1.56 long, 1.08 wide. Abdomen 6.2 long, 2.64 wide. First femur 2.5 long. Chelicerae with 4 (+2 small) prolateral and 3 (+1 small) retrolateral teeth, and approximately 20 denticles in between. Palpal tarsus not conical (width/length = 0.35; Fig. 15). Epigynum as in Figs. 6–8.

Variation.—*Female* (n = 3, including the published data of Lessert and measurements of the two females examined here): Cephalothorax length 3.78–4.2. Total length 9.05–12.21. The coloration of the female abdomen dorsum varies substantially from the lectotype (pale) and the female from Ivory Coast (darker), but the general pattern is the same (Fig. 2). Two small denticles of the cheliceral promargin and one denticle of the retromargin in the lectotype observed as smaller and not in the same line with other denticles are clearly homologous to the more pronounced denticles in the female from Ivory Coast. The number of male cheliceral retrolateral denticles varied in the same specimen (3 on one side and 4 on the other).

Additional material examined.—IVORY COAST: Lamto, XII.1974, 1♂, R. Jocqué, in RMCA, no. 149.800; Lamto, V.1962, 1♀, L. Bigot, in RMCA, no. 131.528.

Distribution.—Western and central Africa.

Singafrotya okavango new species

Figs. 9–12, 17

Types.—Holotype male and paratype female from BOTSWANA: Okavango swamps, Xugana Lagoon, approx. 19°00'S, 23°00'E, 1978, U. Wilmot, in NMP, no. 11720. 3 female paratypes from BOTSWANA: Okavango Delta, Lechwee Camp, 19°02'S, 23°15'E, 130 km N of Maun, Mopane forest margin and Okavango Delta margin, 16–17 November 1980, B. H. Lamoral, in NMP.

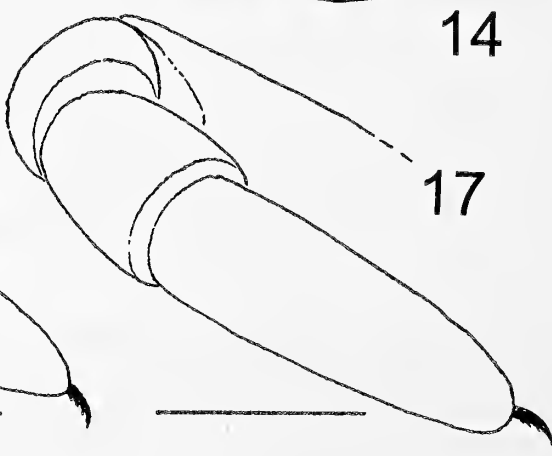
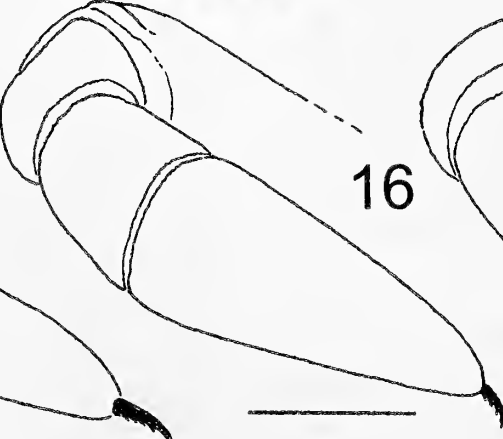
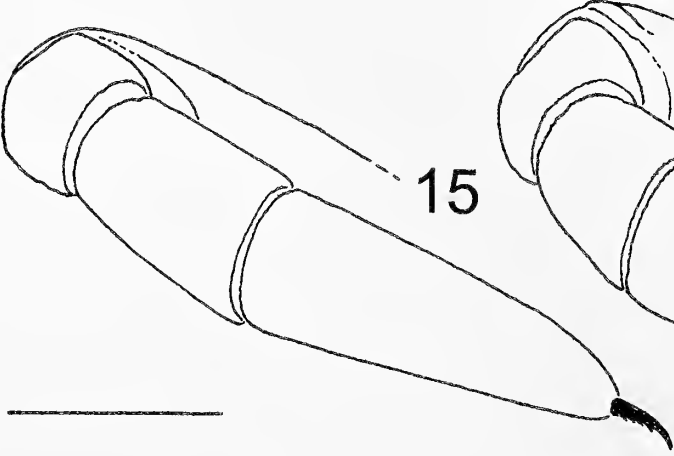
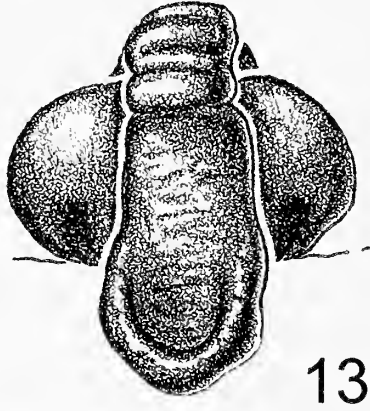
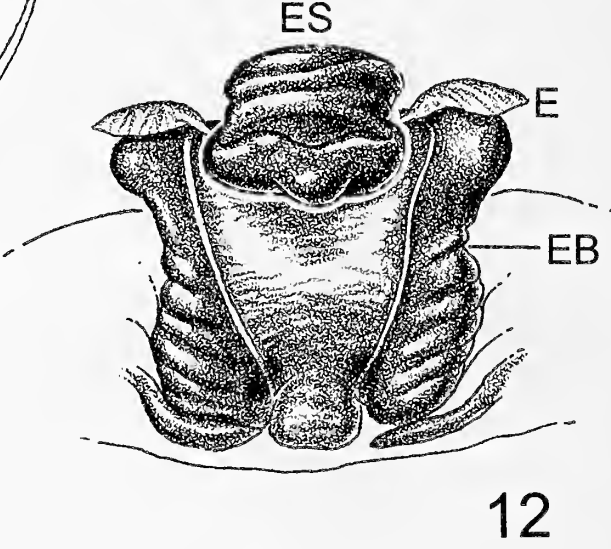
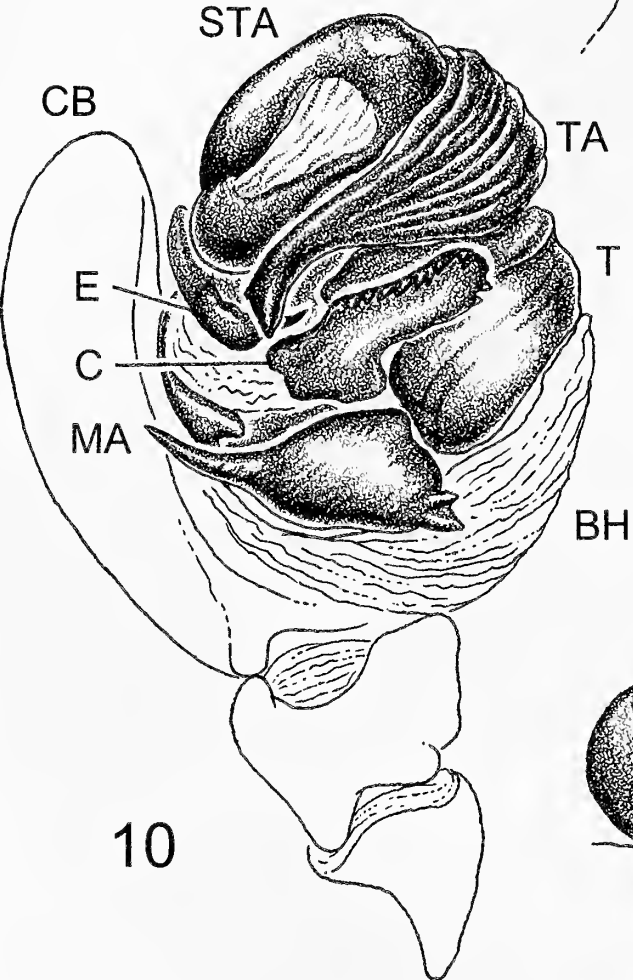
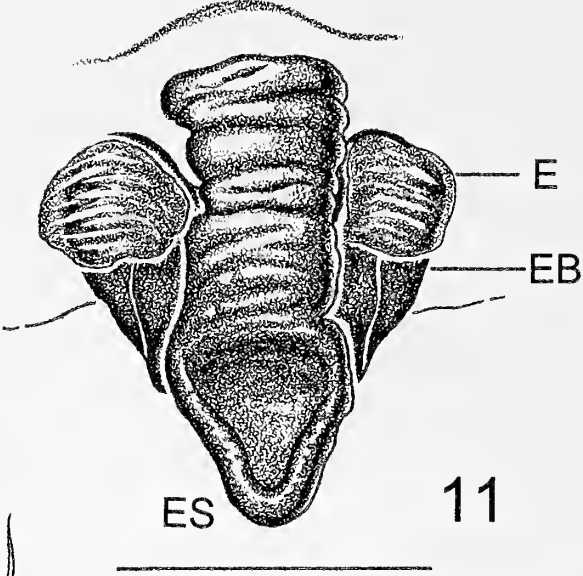
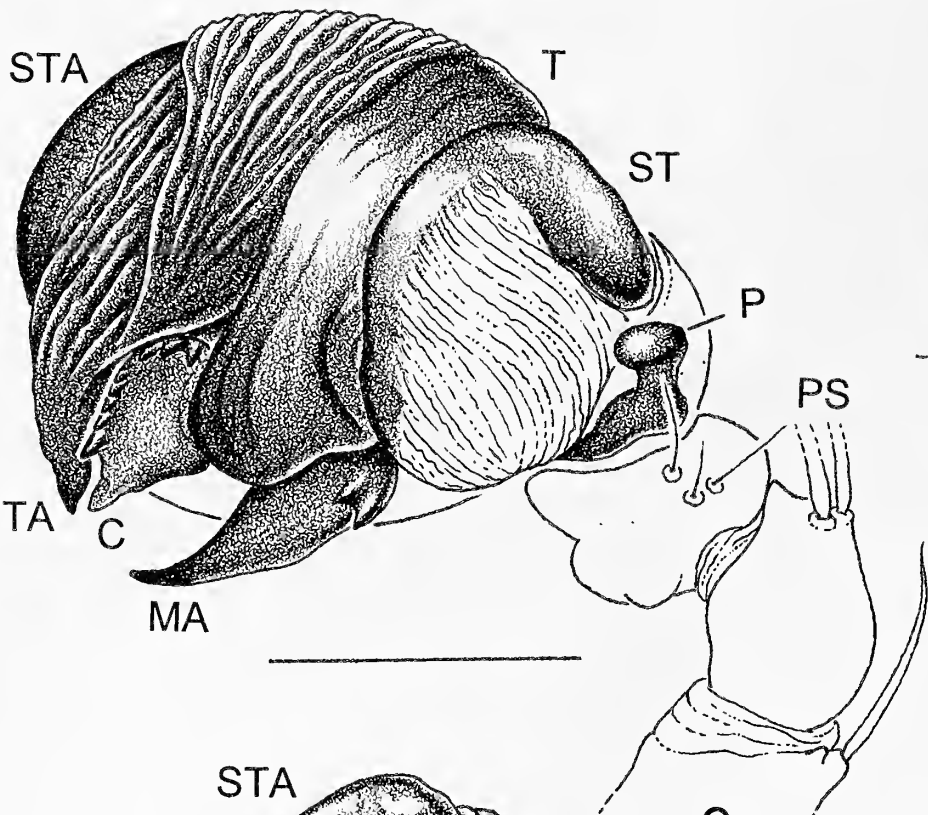
Etymology.—The species is named after Okavango Delta, its type locality. The specific epithet is a noun in apposition.

Diagnosis.—Males of *S. okavango* can be distinguished from those of *S. acanthopus* by the longer and curved terminal apophysis (Figs. 9–10), smaller embolus, not resting on the conductor notch (although this may be due to the fact that the palps of the only available male of *S. okavango* were partly expanded), marginal teeth of conductor pointing mesally (apically in *S. acanthopus*).

Singafrotya okavango females can be distinguished from *S. mandela* by the absence of stout macrosetae on palpal tarsus, and the absence of stout short macrosetae laterally on paturon, both present in the latter species. *Singafrotya okavango* differs from both *S. acanthopus* and *S. mandela* by the heart-shaped epigynum base (Figs. 11–12) with copulatory openings (ventral view) in the anterior part of the epigynum base unlike in both other species. Scape with many wrinkles (fewer in *S. mandela*).

Description.—*Male* (holotype, Figs. 9–10): Total length 7.49. Cephalothorax 3.47 long, 2.38 wide, 0.75 high. Sternum 1.56 long, 0.97 wide. Abdomen 4.26 long, 2.28 wide. First femur 3.13 long. Chelicerae with 5 prolateral and 3 retrolateral teeth, and approximately 12 denticles in between. Pedipalp as in Figs. 9–10.

Female (paratype from Xugana Lagoon, Figs. 11–12, 17): Total length 9.61. Cephalothorax 3.9 long, 2.38 wide, 1.19 high. Sternum 1.64 long, 1.13 wide. Abdomen 6.51 long, 3.13 wide. First femur 2.95 long. Chelicerae with 5 prolateral and 3 retrolateral teeth, and approximately 30 denticles in between. Palpal tarsus not conical (width/length = 0.33; Fig. 17). Epigynum as in Figs. 11–12. General so-



matic morphology except for the diagnostic characters is as in *S. acanthopus* (Figs. 1–3).

Variation.—*Female* (n = 4): Total length 9.61–14.57. Cephalothorax 3.9–5.05 long, 2.38–3.14 wide, 1.19–1.6 high. Sternum 1.64–2.25 long, 1.13–1.36 wide. Abdomen 6.51–10.23 long, 3.13–4.9 wide. First femur 2.95–4.1 long.

Additional material examined.—None.

Distribution.—Okavango Delta, Botswana.

Singafrotypa mandela new species
Figs. 13–14, 16

Types.—Holotype female from SOUTH AFRICA: near Cape Town (no further data), in NMP.

Etymology.—The species is named after Nelson Mandela in honor of his struggle against Apartheid. The specific epithet is a noun in apposition.

Diagnosis.—*Singafrotypa mandela* female can be distinguished from *S. acanthopus* and *S. okavango* by the presence of stout macrosetae on palpal tarsus, stout short macrosetae laterally on paturon, both absent in the latter two species. Epigynum base not heart-shaped (Figs. 13, 14) as in *S. okavango*, copulatory openings in the lower (posterior) part of the epigynum base (ventral view) unlike in both other species, and scape with fewer wrinkles. Posterior epigynal median plate (Fig. 14) wider than in *S. acanthopus* and *S. okavango* (Figs. 8, 12).

Description.—*Female* (holotype, Figs. 13–14, 16): Total length 9.3. Cephalothorax 3.9 long, 2.5 wide, 1.13 high. Sternum 1.56 long, 1.06 wide. Abdomen 6.63 long, 3.13 wide. First femur 2.63 long. Palpal tarsus conical (width/length = 0.44; Fig. 16). Epigynum as in Figs. 13–14. General somatic morphology except for the diagnostic characters as in *S. acanthopus* (Figs. 1–2), but the species is smaller.

Additional material examined.—None.

Distribution.—Cape Town region in South Africa.

Misplaced taxa
Neoscona goliath (Benoit 1963)
new combination

Singafrotypa goliath Benoit 1963: 30–32, figs. 1, 2, female; Platnick 1993: 380.

Types.—Benoit's (1963) female holotype in RMCA is lost (R. Jocqué, *in litt.*).

Diagnosis.—*Neoscona goliath* can be distinguished from other African *Neoscona* species (cf. Grasshoff 1986) by the following female characteristics described here from the illustrations of the female holotype of Benoit (1963: 30, figs. 1, 2): absence of abdominal humps, the abdomen as long as wide and rounded, the extremely narrow eye region, and the shape of the epigynal scape, which is long and narrow, narrowest in the middle, not apically (cf. species of the subgenus *Afraranea* in Grasshoff 1986). The latter characteristic separates *N. goliath* from the similar *Neoscona penicillipes* (Karsch 1879) of central and western Africa.

Distribution.—Ivory Coast. The only record of the species is that of the lost holotype.

Comments.—*Neoscona goliath* exhibits morphology of the genus *Neoscona* (cf. Grasshoff 1986), namely the narrow eye region and a long unwrinkled epigynal scape and lacks the folded scape of the epigynum, wide head region of the carapace and abdomen longer than wide characteristic of *Singafrotypa*.

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←

Figures 9–12.—*Singafrotypa okavango* new species 9–10. Left male palpus (holotype from Xugana Lagoon); 9. Ectal; 10. Mesal; 11–12. Epigynum (female paratype from Xugana Lagoon)—Note male embolus stuck in each copulatory opening; 11. Ventral; 12. Caudal.

Figures 13–14. *Singafrotypa mandela* new species, female epigynum (holotype from Cape Town). 13. Ventral; 14. Caudal.

Figures 15–17. Female pedipalps. 15. *Singafrotypa acanthopus* (Simon); 16. *Singafrotypa mandela* new species; 17. *Singafrotypa okavango* new species. Scale bars = 0.5 mm. Abbreviations as in Figs. 4–8.

MCSNG). We thank Herbert Levi, Nikolaj Scharff and Jonathan Coddington for their useful comments; the latter two made their character data available for reanalysis. Ingi Agnarsson, Jeremy Miller and Fernando Alvarez also provided comments and suggestions at various stages of this work. We thank Mark Harvey, Herbert Levi, Petra Sierwald, and an anonymous referee for their comments on the manuscript. This project was supported by a U.S. National Science Foundation grant (DEB-9712353) and by a Research Enhancement Fund grant from The George Washington University. The first author acknowledges support of the Slovenian Ministry of Science and the Institute of Biology of the Slovene Academy of Sciences and Arts.

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THE COPULATORY ORGANS OF THE CRYPTIC SPECIES *LYCOSA THORELLI* AND *LYCOSA CARBONELLI* AND THEIR HYBRID PROGENY, WITH NOTES ON THEIR TAXONOMY (ARANEAE, LYCOSIDAE)

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ABSTRACT. The copulatory organs of the cryptic species *Lycosa thorelli* and *Lycosa carbonelli* are studied and are shown to exhibit some differences. The morphology of the epigynum, vulva and palpal organs of *L. carbonelli* are here described for the first time. Additional morphological data of these species are provided and the specific diagnosis reformulated. Measurements indicated that the copulatory organs of *L. carbonelli* are larger than *L. thorelli*. Morphological comparison between the parental species and the hybrid progeny show that hybrids are intermediate in morphology and size. The reproductive isolation in these cryptic species and the inheritance of the sexual characters in the hybrid progeny are discussed.

Keywords: *Lycosa carbonelli*, *L. thorelli*, copulatory organs, taxonomy, hybrids

Lycosa thorelli (Keyserling 1877) and *Lycosa carbonelli* Costa & Capocasale 1984 are two cryptic species distinguished by their sexual behavior, mainly by their courtship behavior (Costa & Capocasale 1984). Additionally, the presence of thin hairs on tarsus I of the male of *L. thorelli* and the absence of such hairs in *L. carbonelli*, was the only morphological character found to differentiate these species. Only the copulatory organs of *L. thorelli* were described because Costa & Capocasale (1984) assumed there were no somatic differences with *L. carbonelli*. Pérez-Miles' (1985) morphometric study of these species using somatic characters established that *L. carbonelli* had leg and body dimensions statistically larger than *L. thorelli*. Costa and Francescoli (1991) experimentally obtained interspecific copulations between these species. Only one of these copulations successfully (with a large male of the smaller sized species and a small female of the larger sized species) resulted in hybrid progeny. They indicated that most of the unsuccessful interspecific copulations were possibly caused by slight mechanical incompatibility between the genitalia of the two species.

Copulatory organs have been widely recognized as useful tools in spider systematics, mainly to diagnose species. Recently, the ge-

nus *Lycosa* Latreille 1804 has been redescribed based on a review of some Palearctic species (Zyuzin et al. 2000) but the Neotropical species are poorly known. This lack of knowledge is especially great in cryptic species. In this study, we attempted to determine if the copulatory incompatibility between *L. thorelli* and *L. carbonelli* is caused by morphological differences of the sexual characters; and how hypothetical differences are segregated in the hybrid progeny. Simó et al. (1999) made a preliminary contribution indicating differences on genital morphology between these species.

METHODS

The specimens studied were the same as those used by Costa & Francescoli (1991), Costa et al. (1992) and Costa et al. (1997) in several experimental studies and identified on the basis of their sexual behavior. A total of 109 individuals of *L. thorelli* (29♂ & 20♀) and *L. carbonelli* (30♂ & 30♀) and 13 hybrids (7♂ & 6♀), was examined and deposited in the collection of Sección Entomología, Facultad de Ciencias, Montevideo (FCE). The SEM studies were made in the Laboratorio de Microscopía Electrónica del Museo de la Plata Argentina (MLP). The types examined are deposited in the following institutions: Museo

Nacional de Historia Natural de Montevideo (MNHN) and British Museum of Natural History, London (BMNH). The maximum length (LE) and width (WE) of the septum of the epigynum and the maximum length (LC) and width (WC) of the cymbium was measured, and their means compared with a Student's *t*-test. Copulatory organs were cleared in clove oil, and the bulbs were expanded with potassium hydroxide (KOH). The terminology used for the copulatory organs follows Sierwald (1989, 1990). For the Student *t*-test the significance level used was $P = 0.05$. All measurements are in millimeters. Abbreviations: BS = base of the spermatheca, CD = copulatory duct, FD = fertilization duct, HS = head of the spermatheca, SE = septum of the epigynum, TA = terminal apophysis.

RESULTS

Interspecific and parental-hybrid comparisons.—The most distinctive morphological interspecific gap found for females was the width of the septum of the epigynum (Figs. 1, 4). The septum is narrower in *L. thorelli* (0.15 ± 0.03 mm, $n = 18$) than in *L. carbonelli* (0.29 ± 0.06 mm, $n = 17$); the statistical comparison resulted in significant differences ($t = 5.26$, $P < 0.001$). Hybrids have intermediate values of septum width (0.22 ± 0.03 mm, $n = 6$), and comparisons with both parental species also showed significant differences: $t = 3.9$, $P < 0.001$ with *L. carbonelli* and $t = 4.25$, $P < 0.001$ with *L. thorelli*. Vulvae did not show very clear interspecific differences (Figs. 2, 5). In males the main interspecific difference was the presence of a curved terminal apophysis in the palpal organ of *L. thorelli*, which is straight in *L. carbonelli* (Figs. 3, 6).

Significant differences were found for all other measurements between the parental species studied: LE, $t = 7.48$, $P < 0.001$; LC, $t = 5.81$, $P < 0.001$; WC, $t = 8.21$, $P < 0.001$. In all cases the analyzed features of the copulatory organs of *L. carbonelli* were significantly larger than in *L. thorelli* ($P < 0.001$). Respectively the means (\pm standard deviation) for *L. carbonelli* and *L. thorelli* were LE: $0.74 (\pm 0.04)$, $0.63 (\pm 0.05)$; LC: $1.88 (\pm 0.15)$, $1.59 (\pm 0.15)$, WC $1.02 (\pm 0.08)$, $0.83 (\pm 0.07)$.

Comparisons of the measurements of the copulatory organs between the hybrids and

each of the parental species showed significant differences between the hybrids and *L. carbonelli* for all the characters compared (in all cases $P < 0.001$). In comparisons between hybrids and *L. thorelli* no significant differences were found for WC and LC, but the comparisons of WE (as mentioned above) and LE ($P < 0.001$) showed significant differences.

Tarsal dorsal hair of leg I, indicated as diagnostic of *L. thorelli*, was found also in *L. carbonelli* (Fig. 7) and in their hybrid progeny. On the basis of the present results we re-diagnose the species below.

Lycosa thorelli (Keyserling 1877)

Figs. 1–3

Tarentula thorelli Keyserling 1877:650; Keyserling 1891:257.

Tarentula sternalis Bertkau 1880:73.

Lycosa thorelli: Petrunkevitch 1911:568; Bonnet 1957:2629; Zimmer 1963:19; Capocasale 1980:65; Costa 1980:67; Costa & Capocasale 1984:428; Pérez-Miles 1985:19; Gudynas & Pérez-Miles 1988:1; Costa & Francescoli 1991:1768; Francescoli & Costa 1992:380; Platnick 1993:489; Platnick 1997:560; Costa et al. 1997:1845; Costa et al. 2000:237.

Lycorma thorelli: Roewer 1954:267

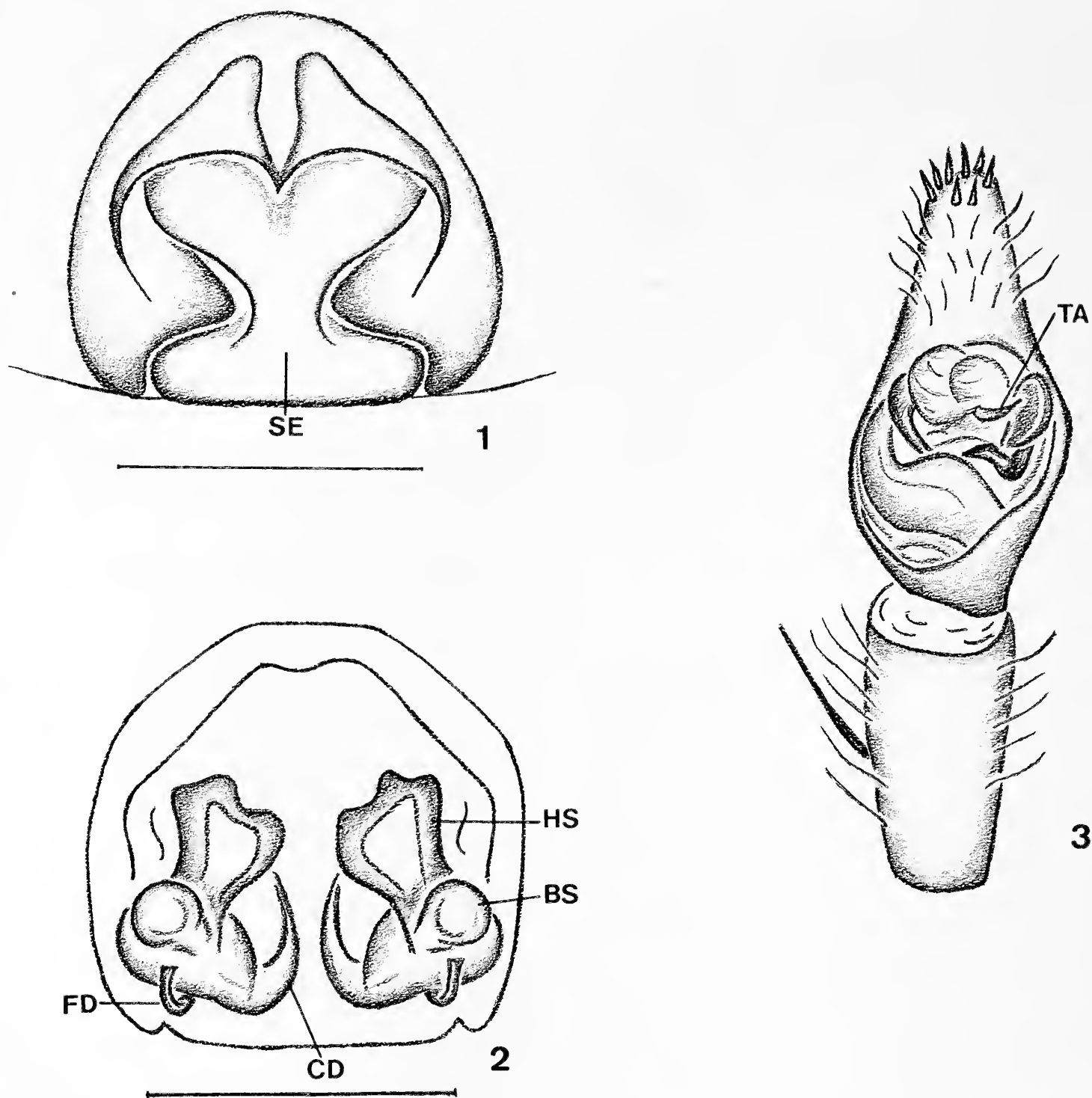
Types.—Two females and one male (syntypes) from Colombia, 1890.7.1.2600–15, examined, deposited in BMNH.

Diagnosis.—Differs from *L. carbonelli* by the intensification of the alternate waving of the forelegs during the second precopulatory phase (see Costa & Francescoli 1991), the presence of a narrow septum on the epigynum (Fig. 1) and by the presence of a curved terminal apophysis (Fig. 3).

Additional material examined.—URUGUAY: *Canelones*; Marindia, 17 November 1996 (Costa, FCE) 1♂; 17 December 1996 (Costa, FCE) 1♂; 11 May 1998 (Costa, FCE) 2♀; 8 October 1998 (Costa, FCE) 3♂; 23 October 1998 (Costa, FCE) 1♀. Rocha. Bocas del Sarandí: 26 August 1994 (Pérez-Miles & Toscano, FCE) 6♀. Sarandí del Consejo, 23 July 1994 (Pérez-Miles & Toscano, FCE) 1♂; 30 September 1994 (Pérez-Miles & Toscano, FCE) 1♀. Potrero Grande: 21 July 1994 (Pérez-Miles & Toscano, FCE) 3♀, 2♂.

Lycosa carbonelli Costa & Capocasale 1984
Figs. 4–7

Lycosa carbonelli Costa & Capocasale 1984:426; Pérez-Miles 1985:19; Gudynas & Pérez-Miles



Figures 1–3.—*Lycosa thorelli* copulatory organs, 1. Epigynum; 2. Vulva; 3. Pedipalp, ventral view. Scale = 0.5 mm.

1988:1; Costa & Francescoli 1991:1768; Francescoli & Costa 1992:380; Platnick 1989:370; Platnick 1993:489; Platnick 1997:560; Costa et al. 1997:1845; Costa et al. 2000:237.

Types.—Male holotype and paratype female from Malvín, Montevideo, (750), May 1977, F. Costa Col., examined, deposited in MNHN.

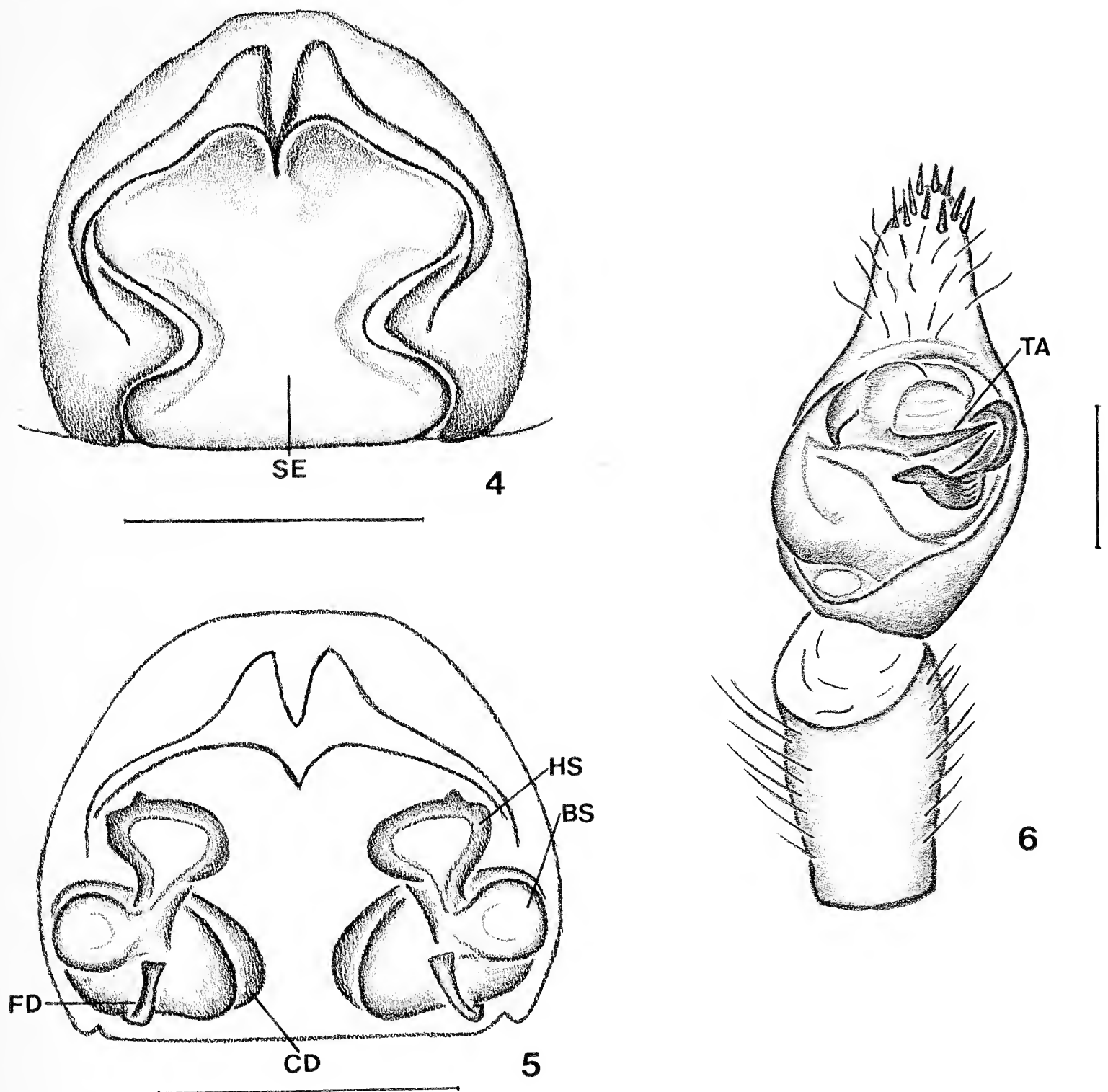
Diagnosis.—Differs from *L. thorelli* by the alternation of “explosive” locomotion with prolonged immobility at the second precopulatory phase (see Costa & Francescoli 1991), the broad septum on the epigynum (Fig. 2) and by the presence of a straight and longer terminal apophysis (Fig. 6).

Additional material examined.—URUGUAY:

Canelones; Marindia, 11 May 1998 (Costa, FCE) 4♂; 25 June 1998 (Costa, FCE) 1♀; 18 October 1996 (Costa, FCE) 1♀; 23 October 1998 (Costa, FCE) 2♀.

DISCUSSION

Stratton & Uetz (1981, 1997) studied three cryptic species of *Schizocosa* Chamberlin 1904 obtaining hybrids in forced copulations. They indicated the importance of courtship isolation mechanisms among these species. Töpfer-Hofmann et al. (2000) studied six closely related cryptic species of *Pardosa* Koch 1847 from Europe. They found that courtship behavior was the main isolating mechanism in at least five of these species. The females could not be reliably distin-



Figures 4–6.—*Lycosa carbonelli* copulatory organs, 4. Epigynum; 5. Vulva; 6. Bulb, ventral view. Scale = 0.5 mm.

guished by their somatic or genitalic characters.

In the two cryptic species studied here, the only morphological difference indicated by Costa & Capocasale (1984) for distinguishing them was the presence of thin hairs on tarsi I of the male of *L. thorelli*, and their absence in *L. carbonelli*. Since we found these hairs in both species we remove it as diagnostic character.

Francescoli & Costa (1992) studied the post-emergence development of *L. carbonelli*, *L. thorelli* and their hybrid progeny. They found that the duration of the development of

the hybrids was intermediate between the parental species, although it was closer to the duration of *L. carbonelli*. In another study, Costa et al. (1997) analyzed the male sexual behavior elicited by a hybrid pheromone, using specimens of *L. carbonelli*, *L. thorelli* and hybrids. They found that hybrid males showed behaviors similar to those of each of the parental species, but their characteristics (units frequency, angle covered by leg movement and standardized duration) were intermediate between the two. Results obtained here show that the morphology of the copulatory organs in hybrids is slightly more related to *L. car-*

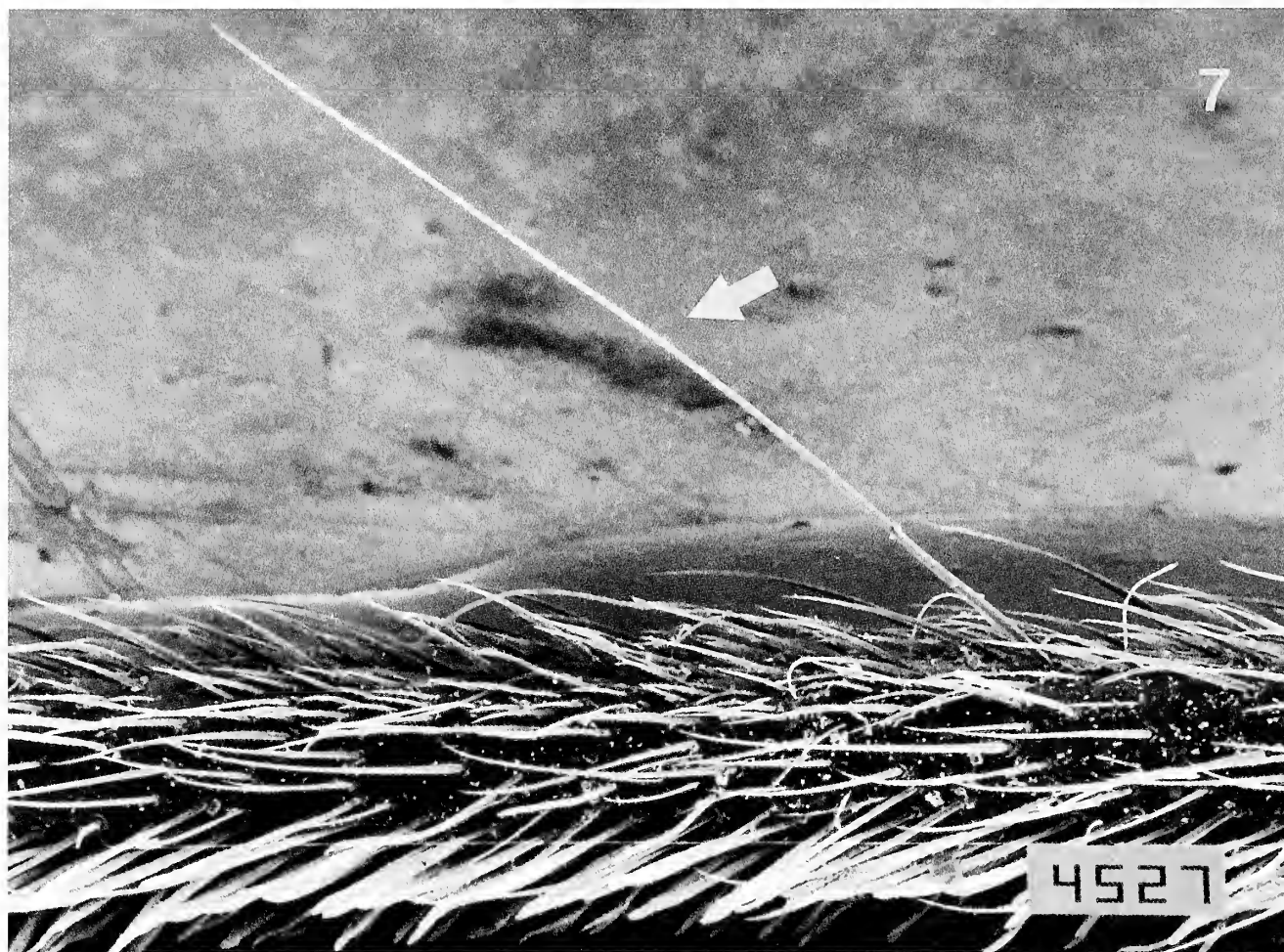


Figure 7.—Left male tarsus I of *Lycosa carbonelli*. The arrow shows one longer hair (see text). 100X. Scale = 1000 μ m.

bonelli. The width of the epigynal septum seems to be a good diagnostic character to distinguish between the species and showed intermediate values in hybrids. These results suggest the polygenic inheritance of such ethological and morphological characters. The mechanical incompatibility between the copulatory organs of *L. carbonelli* and *L. thorelli* indicated by Costa & Francescoli (1991) could be explained by the morphological and morphometric differences demonstrated here.

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ADULT SIZE OF EIGHT HUNTING SPIDER SPECIES IN CENTRAL AMAZONIA: TEMPORAL VARIATIONS AND SEXUAL DIMORPHISMS

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ABSTRACT. We studied temporal variation in adult size and sexual size dimorphism (SSD) of seven hunting spider species, *Ctenus amphora*, *C. crulsi*, *C. manauara*, *C. villasboasi* (Ctenidae), *Phoneutria fera*, *P. reidyi* (Ctenidae), and *Ancylometes rufus* (Pisauridae) in a tropical rainforest, and one species from a relatively open vegetation habitat, *C. minor*, in central Amazonia. Size variation was great within and among field trips. Spiders were generally smaller in October (end of dry season) when compared with other months: adults of *C. amphora*, *C. crulsi* and *C. manauara* were significantly smaller in October 1995 when compared to February 1996; *P. fera* were smaller in October 1998 than in June 1998; and *A. rufus* were smaller in October 1998 than in August 1998. The temporal variation in size is possibly a result of low prey availability during the dry season. Six species had significant differences in prosoma length between males and females: *C. amphora*, *C. crulsi*, *C. manauara* and *C. minor* had larger males (which is considered rare in spiders), and *P. reidyi* and *P. fera* had larger females. However, considering an alternative index of size, the “rough area” (an approximate measure of the area of the spider as seen from above), the males were significantly larger for all species (up to 2.8 times in *C. minor*), because they have longer legs relative to their prosoma length. We suggest that selection for high mobility may be the reason for adult males with longer legs, and that the smaller species had higher degrees of sexual dimorphism in leg length because of the relative size of obstacles in the leaf litter.

RESUMO. Estudamos a variação temporal de tamanho de adultos e o dimorfismo sexual de tamanho de sete espécies simpátricas de aranhas errantes, *Ctenus amphora*, *C. crulsi*, *C. manauara*, *C. villasboasi* (Ctenidae), *Phoneutria fera*, *P. reidyi* (Ctenidae), e *Ancylometes rufus* (Pisauridae) em uma floresta tropical úmida, e uma espécie em um habitat de vegetação relativamente aberta, *C. minor*, na Amazônia Central. A variação de tamanho foi grande dentro e entre excursões de coleta. As aranhas foram geralmente menores em outubro (final da estação seca) comparado com outros meses: adultos de *C. amphora*, *C. crulsi*, *C. manauara* e *C. minor* foram significativamente menores em outubro de 1995 comparado a fevereiro de 1996; *P. fera* foram menores em outubro de 1998 do que em junho de 1998 e *A. rufus* foram menores em outubro de 1998 do que em agosto de 1998. A variação temporal em tamanhos observada é possivelmente um resultado de baixa disponibilidade de presas durante a estação seca. Seis espécies tiveram diferenças significativas em comprimento do cefalotórax entre machos e fêmeas, *C. amphora*, *C. crulsi*, *C. manauara* e *C. minor* tiveram machos maiores (o que é considerado raro em aranhas), *P. reidyi* e *P. fera* tiveram fêmeas maiores. Entretanto, considerando um índice alternativo de tamanho, a “área aproximada” (uma medida da área da aranha em vista superior), os machos foram significativamente maiores em todas as espécies (até 2,8 vezes em *C. minor*), porque eles têm pernas mais longas em relação ao tamanho do cefalotórax. Nós sugerimos que uma seleção para alta mobilidade pode ser a razão para machos com pernas maiores, e que as menores espécies tem maior dimorfismo sexual no comprimento das pernas devido ao tamanho relativo dos obstáculos na serapilheira.

Keywords: *Ancylometes*, *Ctenus*, Ctenidae, *Phoneutria*, Pisauridae, seasonality, sex ratio, sexual-size-dimorphism, wandering spiders

The size of adult spiders may vary considerably in individuals of the same species and sex. Studies on such variation contributed to the evaluation of spatial and temporal variation in spider growth and abundance (e.g. Jocqué 1981a, b; Olive 1981; Vollrath 1988; Vertainen et al. 2000), and to the discussion of food limitation in spiders (Wise 1993). However, there are relatively few studies documenting spatial and temporal size variation in tropical hunting spiders.

Besides the variation in the size of spiders of the same sex, the differences in size between sexes are remarkable in some species, and the reasons for sexual dimorphism in spiders have received much attention (e. g. Petersen 1950; Jocqué 1983; Elgar 1991; Vollrath & Parker 1992; Head 1995; Prenter et al. 1997; Prenter et al. 1999; Coddington et al. 1997; Hormiga et al. 2000; Schneider 1997; Schneider et al. 2000, Vertainen et al. 2000). Prenter et al. (1999) argued that fecundity selection provides the only general explanation for the evolution of sexual dimorphism in spiders. However, most studies focused on the selective pressures for different degrees of dimorphism in which females are larger; less attention has been paid to the phenomenon that males are slightly larger in a few species.

We studied the temporal variation in the size of adults and the degree of sexual size dimorphism of seven ground hunting spider species in a tropical forest: *Ctenus manauara* Höfer, Brescovit & Gasnier 1994 (Ctenidae), *C. amphora* Mello-Leitão 1930, *C. crulsi* Mello-Leitão 1930, *C. villasboasi*, Mello-Leitão 1949, *Phoneutria fera* Perty 1833 (Ctenidae), *P. reidyi* (F. O. P.-Cambridge 1897) and *Ancylometes rufus* (Walckenaer 1837) (Pisauridae). These species are sympatric in our main study area ("Reserva Ducke"); however, they have differences in relative abundance among habitats and microhabitats. The *Ctenus* species forage exclusively ambushing on the ground litter, but *C. manauara* and *C. crulsi* are more abundant in dry clay soils areas, *C. amphora* more abundant in dry sandy soil areas, and *C. villasboasi* has a more homogeneous distribution including dry and wet clay and sandy soils (Gasnier & Höfer 2001). The *Phoneutria* species forage on the vegetation as young juveniles, and on the ground and on the vegetation when late instar juveniles or adults. *Phoneutria reidyi* is almost absent on dry

sandy soils while *P. fera* is well distributed in dry and wet sandy and clay soils (Torres-Sanches 2000). *Ancylometes rufus* forage exclusively on the ground, where they feed mostly on arthropods, close to or far from bodies of water; however, it is much more abundant close to streams and natural pools, where they find extra food (e.g., tadpoles, toads and small fishes) and may dive to escape from predators (Azevedo 2000; Höfer & Brescovit 2000). These species, specially the *Ctenus* in the dry areas and *A. rufus* in the wet areas, are the dominant medium to large sized hunting spiders in "Reserva Ducke." Another species, *Ctenus minor* F. O. P.-Cambridge 1897, was included in the evaluation of size dimorphism. It forages on the ground in places with a relatively open vegetation on dry sandy soils locally called "campina" (Höfer et al. 1994). This species was collected about 100 km from "Reserva Ducke" (see Methods).

METHODS

Most of the study was conducted in "Reserva Florestal Adolpho Ducke" (2°57' S, 59° 57'W), a forest reserve in contact with the city of Manaus, Amazonia, Brazil. The reserve has 10,000 ha of "terra-firme" primary forest (description of vegetation in Guillaumet 1987). We collected data in an area inside the reserve of about 2 by 5 km, where three different habitats occur: "Baixio," or forest close to streams in small flat valleys on hydromorphic soils; "Campinarana," or forest on dry sandy soils, and "terra-firme forest" in a strict-sense, on dry clay soils. A more detailed description of the study area is presented in Gasnier & Höfer (2001). The wettest months are November–May, the driest June–October, and the mean annual rainfall is 2480 mm (Marques-Filho et al. 1981). We collected *C. minor* in the "Reserva da Campina" (01° 40'S, 60° 50'W). This species apparently occurs in "Reserva Ducke," but not in the area where we collected spiders. We included data on *C. villasboasi* collected by L. Mestre in "Reserva Ducke" and in the reserves of the "Projeto de Dinâmica Biológica de Fragmentos Florestais" (02°38'S, 59° 93'W).

Data presented here were part of one doctoral and two master dissertations on *Ctenus* (Gasnier 1996), *Phoneutria* (Torres-Sanchez 2000) and *Ancylometes* (Azevedo 2000), which are deposited (with the raw data) in the

library of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Therefore, there are some differences in the methods and time of collection. We searched for spiders with head lamps at night, their active period. Spiders of the genus *Ctenus* were collected by forcing them to enter small glass vials for identification and measurement of the prosoma length. The measurement was made with a ruler in the field, because collection of individuals was avoided during the study. Comparing field and laboratory measures, we considered this to be a sufficiently accurate method even for the smallest species *C. manauara*, since the same person did all measurements. Spiders of the genus *Phoneutria* were collected with a plastic vial large enough for a safe catch, and killed in the place of the capture with 70% alcohol for later identification and measurement of the prosoma length. *Ancylometes rufus* were immobilized by hand and measured in the field with a ruler (always by the same person), because the study of this genus included the marking and recapture of the spiders.

We used prosoma length as our main index of size instead of prosoma width, a more standard measure of spider size (Jocqué 1981b), because the prosomas of these spiders are elongate, and we considered it a more accurate measure when it has to be done in the field with a ruler, as we did for *Ctenus*, and we maintained it for the other spiders. A factor to transform prosoma length into an approximate measure of prosoma width for all these spiders for comparative studies is 0.8. A second index of size was the "rough area" (RA), which was an area of a circle (πr^2) calculated using the mean of the leg lengths (fully spread) as radius (r). This index is a simplified measure of the area of a spider as seen from above; unlike the former index, this measure of size takes into account the lengths of the spiders' legs. We also calculated an index of the length of legs corrected by size, the leg/prosoma ratio (LPR), which was the mean of the leg lengths divided by the prosoma length. We decided to use the latter indices after field work, therefore the evaluations with these indices were restricted to the study of the degree of sexual dimorphism, and the measurements were from the spiders that we deposited in the Arachnological Collection of INPA as vouchers (INPA 001–INPA 063 and "lote TG01"),

from Reserva Ducke and other from the region close to Manaus. Spiders without at least one leg of each pair intact were not measured. For all these indices, we calculated the degree of sexual size dimorphism (SSD) as the mean of the index of the males divided by the mean of the females. We also calculated the maximum prosoma length differences (MD) as percentages as follows: $MD = 100 * (\text{largest size} - \text{smallest size}) / \text{smallest size}$.

We measured the prosoma length of *Ctenus* found along 12 km of trails inside primary forest that included the three different habitats types of the reserve in October 1995 and in February 1996. We included extra data of *C. villasboasi* (see above) in the analysis of SSD, because sample size of adults of this species was low. *Phoneutria* were collected, along 9 km of trails (mostly the same used in the *Ctenus* study) in June and October of 1998 and April and August of 1999, and in other places of the reserve in the same years. We used all data of this genus for evaluation of SSD, but only the data of the trails in the evaluation of temporal variation of size, to avoid an influence of combining data from different localities in the evaluation. Furthermore, we only used data of field trips in which more than five adults of the considered species were collected. *Ancylometes rufus* were measured along 0.5 km of the stream "Barro Branco," from 1 km above the administration building of the reserve. We made bimonthly field trips from June 1998–August 1999, but we used only data from June–October of 1998 in the analysis of temporal variation of size, because in the other months we could not find more than five adults in a trip.

We used a non-parametric ANOVA (Mann-Whitney U test and Kruskal Wallis KW) to test the differences of sizes between sexes and among field trips, and Mann-Whitney corrected by Bonferroni for multiple pairwise comparisons (Zar 1984), which were made only between one trip and the next to reduce the number of comparisons. The significance level was $\alpha = 0.05$, but we generally presented exact values, and the significance levels were adjusted to 0.025 for two comparisons and to 0.017 for three comparisons. The presented indices of the calculated U and KW are the number of cases in each category in order of time or first males then females. We did not use evolutionary covariance regression (Head

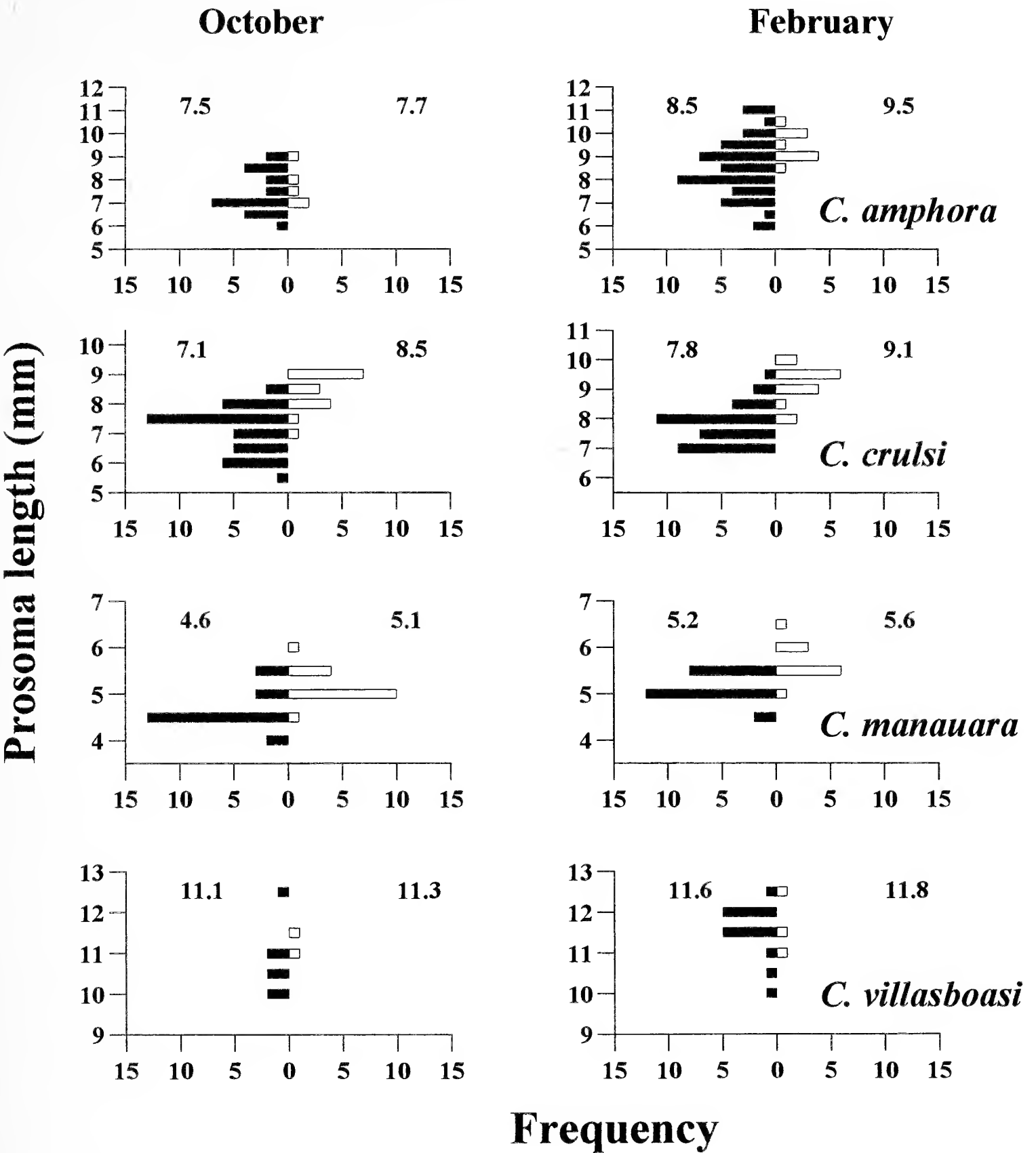


Figure 1.—Frequency distribution of prosoma length classes of four *Ctenus* species in October 1995 and February 1996. Closed bars = females, open bars = males. The numbers are the mean size for each sex in each occasion.

1995), or any other comparative biology method to correct for inflated degrees of freedom, for the relationships between RA and prosoma length, and between LPR and prosoma length, because the phylogenetic relationship among these genera is still controversial (Huber et al. 1993), and among species in *Ctenus* is unknown. All measures of prosoma length are in mm.

RESULTS

We observed significant temporal variation in size for most species. Spiders of three *Ctenus* species were significantly smaller in October 1995 compared to February 1996 (*C. amphora*, $U_{27,55} = 334$, $P < 0.001$; *C. crulsi*, $U_{55,50} = 883$, $P = 0.001$; *C. manauara*, $U_{41,34} = 339$, $P < 0.001$; *C. villasboasi*, $U_{10,14} = 43$, $P = 0.11$; Fig. 1). Size varied for *P. fera*

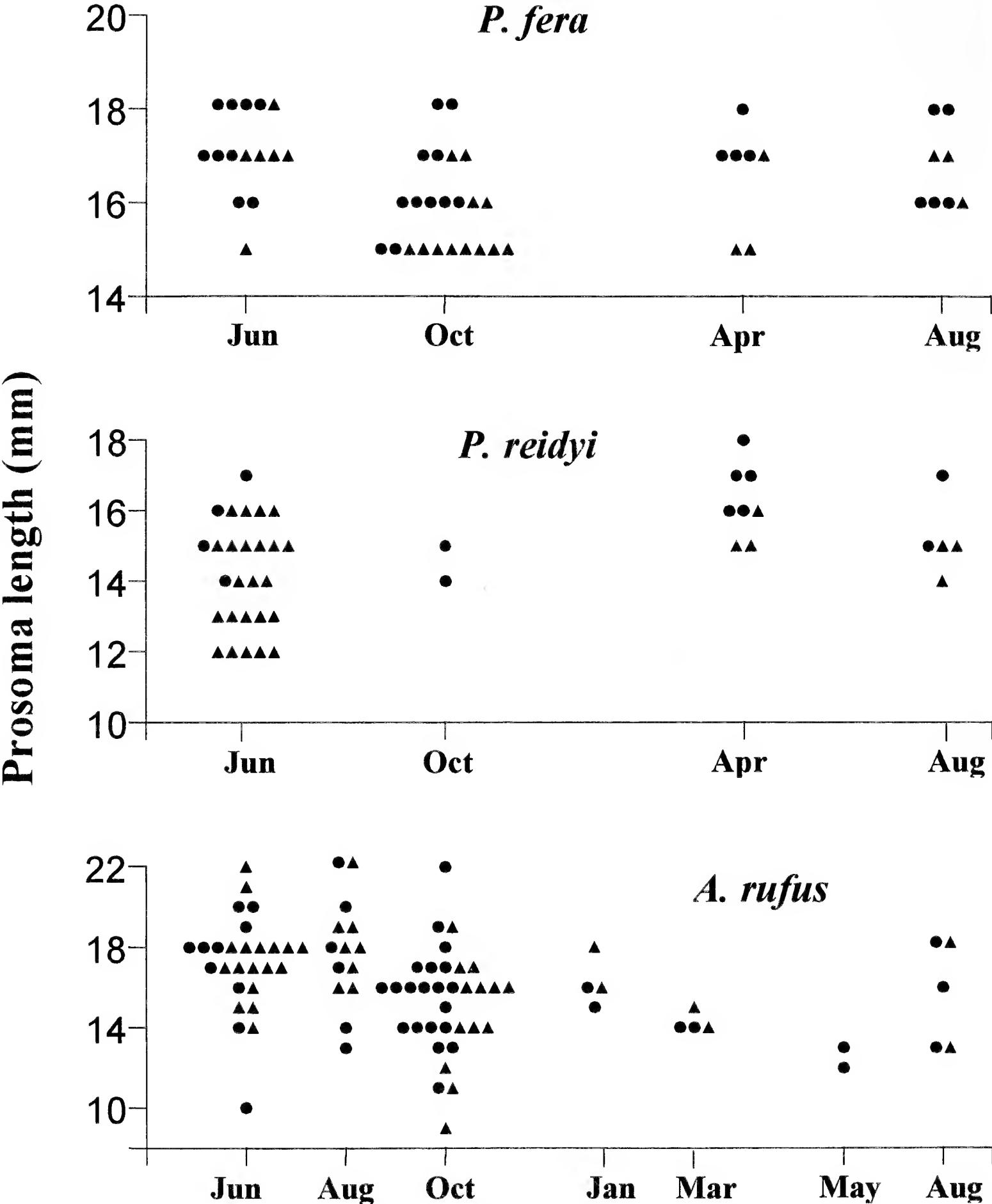


Figure 2.—Prosoma length of females (●) and males (▲) of adults of *Phoneutria fera*, *P. reidyi* and *Ancylometes rufus* on each field trip.

($KW_{15,23,7,8} = 11.6$, $P = 0.009$), with the following differences of means on the pairwise comparisons: June 1998 (17.1) > October 1998 (15.9) = April 1999 (16.6) = August 1999 (16.8) (Fig. 2). Only in June 1998 and April 1999 did we collect enough adults of *P.*

reidyi for evaluation, and we found larger adults in April ($U_{27,8} = 35.5$, $P = 0.002$, respectively 14.2 and 16.3). However, an unusual sex ratio was found on the first field trip (Table 1); 85% of the adults were males, compared to 46% in the other three months, and

Table 1.—Size data of the spiders measured in the field. *n*1, *n*2, *n*3 and *n*4 = sample size of females and males respectively in each field trip (see text for field trip dates in each genus); MPLF = mean prosoma length for females; MPLM = mean prosoma length for males; StD = standard deviation; MDF = maximum prosoma length difference for females (percentages); MDM = maximum prosoma length difference for males; SDPL1 = degree of size dimorphism in prosoma length (first sample); Significance levels of SDPL1: **P* < 0.05, ***P* < 0.01, ****P* < 0.005, ns = non significant.

Species	<i>n</i> 1	<i>n</i> 2	<i>n</i> 3	<i>n</i> 4	MPLF	StD	MPLM	StD	MDF	MDM	SDPL1	Sign
<i>C. manauara</i>	22:19	22:12			4.90	0.46	5.32	0.44	38	44	1.09	***
<i>C. crulsi</i>	38:17	34:16			7.46	0.79	8.76	0.7	73	43	1.17	***
<i>C. amphora</i>	22:5	45:10			8.15	1.25	8.87	1.09	83	50	1.09	*
<i>C. villasboasi</i>	8:2	11:3			11.4	0.93	11.6	0.65	44	25	1.02	ns
<i>P. reidyi</i>	4:23	2:0	5:3	2:3	15.9	1.26	14.2	1.39	36	75	0.89	***
<i>P. fera</i>	9:6	11:12	4:3	5:3	16.8	0.97	16.2	1.28	20	20	0.96	**
<i>A. rufus</i>	10:17	6:8	20:13		16.0	2.71	16.5	2.57	144	133	1.03	ns

this species presented sexual size dimorphism in prosoma length (see below). Therefore, this difference probably does not reflect the variation in the size of the spiders, but rather the change in the sex ratio in our captures. This was not a problem in the analysis of *P. fera*, because sex ratio was approximately constant among trips to the field, and no size dimorphism was detected for *A. rufus* (see below). The size of the adults of *A. rufus* varied from June to October 1998 ($KW_{27,14,33} = 14.6$, $P < 0.001$), with the following differences in pairwise comparisons: June (17.3) = August (17.8) > October (15.3).

Adult males had a prosoma length significantly larger than females in three species of *Ctenus*: *C. amphora* ($U_{15,67} = 682$, $P = 0.030$), *C. crulsi* ($U_{33,72} = 2110$, $P < 0.001$), and *C. manauara* ($U_{31,44} = 986$, $P < 0.001$) (Table 1). Significant difference in prosoma length between sexes was not found for *C. villas-*

boasi, neither for those collected in October 1995 or February 1996 ($U_{5,19} = 54$, $P = 0.64$), nor for more than 36 females and 17 males measured on other occasions (see methods; $U_{22,55} = 750$, $P = 0.09$). Both *Phoneutria* species had females with larger prosoma length: *P. reidyi* ($U_{29,13} = 72$, $P = 0.001$) and *P. fera* ($U_{24,29} = 200$, $P = 0.006$). There was no significant difference in prosoma length between males and females of *A. rufus* ($U_{44,45} = 1135$, $P = 0.23$). The degrees of sexual dimorphism in prosoma length of the spiders measured in the field (SDPL1- Table 1) were similar to those from the Arachnological Collection of INPA (SDPL2- Table 2).

Although some species had females with greater prosoma length, all species had males with larger “rough area” (RA) (Table 2, $P < 0.05$ for *U* test), because they all had legs significantly longer relative to their prosoma lengths ($P < 0.05$). *Ctenus minor* had males

Table 2.—Size data of the spiders measured in the Arachnological Collection of INPA. *n* = sample size of females and males respectively; MFPL = mean female prosoma length; MMPL = mean male prosoma length; StD = standard deviation; SDPL2 = degree of sexual dimorphism in prosoma length (second sample); SDRA = degree of sexual dimorphism in “rough area” (see text); SDLPR = degree of sexual dimorphism in leg/prosoma ratio.

Species	<i>n</i>	MFPL	StD	MMPL	StD	SDPL2	SDRA	SDLPR
<i>C. minor</i>	15:16	4.33	0.56	4.81	0.60	1.11	2.78	1.53
<i>C. manauara</i>	41:28	4.59	0.45	5.00	0.47	1.09	2.52	1.46
<i>C. crulsi</i>	20:12	7.15	0.61	8.13	0.53	1.14	2.54	1.40
<i>C. amphora</i>	8:10	7.55	0.72	8.63	0.44	1.14	2.45	1.37
<i>C. villasboasi</i>	3:3	11.3	1.15	11.7	0.58	1.02	2.14	1.42
<i>P. reidyi</i>	6:6	16.2	1.72	14.3	1.97	0.95	1.33	1.31
<i>P. fera</i>	6:6	17.7	1.03	16.8	1.47	0.87	1.32	1.21
<i>A. rufus</i>	4:4	17.5	1.73	16.6	1.75	0.95	1.63	1.35

significantly larger in all indices ($P < 0.05$). This dimorphism in RA and LPR is evident even by sight in the field (specially for *Ctenus*), and occurs when the males become adults; we could not distinguish a female from a male of an instar before maturity based on the relative size of the legs. The degree of sexual size dimorphism in RA and LPR decreased significantly with the female prosoma length of the eight species ($r^2 = 0.92$; $P < 0.001$ for RA and $r^2 = 0.68$; $P = 0.007$ for LPR).

DISCUSSION

The size variation of these species within an area of 10 km² was remarkable: the mean difference in prosoma length between the largest and smallest individuals for females was 63%. Based on the relationship between length and size for immature *Phoneutria*, we estimate that this variation in length is equivalent to a difference of almost four times in weight, and that the variation found in *A. rufus* between the largest and the smallest adult females is greater than 10 times in weight. Jocqué (1981) found similar size and weight variations, and our results corroborate his suggestion that large size variations among individuals are a rule rather than an exception in spider populations. Laboratory studies have shown that the size of adults depends on the amount of food during development (e. g. Nakamura 1987; Vertainen et al. 2000), and this probably also explains most of the intraspecific spatial and temporal variation in the size of spiders in nature (Jocqué 1981 a, b; Wise 1993). Therefore, the observed size variation reflects a great phenotypic plasticity which may be important for habitats with unpredictable food supply in space and time.

There is evidence that seasonality in the availability of prey causes variation in size for these spiders. Most species had smaller adult sizes in October, the end of the dry season, when the abundance of the arthropods in the leaf litter in this forest is considered low (Luizão & Luizão 1991). Even the abundance of *Ctenus* and *Phoneutria* is smaller during the dry season (Gasnier & Höfer 2001; Torres-Sanchez 2000). Assuming a significant level of mortality, specially for the smaller species, most of the adults found in this month probably developed mostly during a period with low availability of prey. In the case of *A. ru-*

fus, availability of food is likely to be larger in the wet season for the additional reason that during this time there are pools close to the streams. *Ancylometes rufus* migrate to pools apparently in search of prey as small fishes, tadpoles and toads, and, latter, in the dry season, they return to the stream borders, where it is probably safer than in the dry pools, but more difficult to capture these prey (Azevedo 2000).

Based on body size (body length), Head (1995) stated that males larger than females is a rare phenomenon, and only with a small degree of size dimorphism. Males larger than females is an exception in the records of sexual dimorphism of spiders: from the 1181 species listed by Head (1995) and Prenter et al. (1997), only about 1% consisted of species with larger males. However, sample size to detect a small size dimorphism should be large, because natural size variation in each sex may be large in spiders, specially if body size is the measure used, instead of prosoma length or width, because the first index also varies with the nutritional and reproductive status of the spider. We believe that further studies with species with smaller degree of sexual dimorphism may show that larger males (in prosoma length) are more common than previously stated. In this study, we contribute with the record of four species (but all from a single genus) to the list of males with greater prosoma length.

Prosoma length (or width) is certainly the most important index of size to start the comprehension of sexual size dimorphism in spiders; however, indices related to the leg lengths are also important (Prenter et al. 1995). Based on the "rough area" (RA), we found that a high degree of sexual dimorphism of size in spiders (up to 2.78 in *C. minor*) is not restricted to larger females. Furthermore, we detected negative correlations between the degree of sexual size dimorphism and prosoma length for the RA and LPR indices. There is an unidentified spider species of the family Heteropodidae in our study area that forages in the leaf litter and is a little smaller than *C. manauara* which also has adult males with legs distinctly longer than the juveniles and adult females (unpublished). It is not clear if these correlations would remain after considering the phylogenetic relationships among these species (Ridley 1989). However, in the

absence of these data, the correlations and the recent observations are enough to suggest that this relationship should be investigated.

Sexual dimorphism may be the result of different selective pressures (Hedrick & Temeles 1989). Males may be larger as a result of the competition for access to mates and to mates' choice, or the dimorphism may have evolved from food competition between sexes, or the sexes may have intrinsic differences between the reproductive roles (such as a more active search for mates by males). Legrand & Morse (2000) suggest that males of a species of crab spiders (*Misumena*) probably evolved relatively longer legs because it would be advantageous for locating females under low density, and Kotiaho et al. (1999) found that large males of *Hydrolycosa rubrofasciata* (Lycosidae) have advantages in mate searching. We believe that the same may apply for the species of the present study. Males of *Ctenus* are much more active than females and juveniles (Salvestrini & Gasnier 2001), which seems to be a common pattern for Ctenidae (Schmitt et al. 1990). Although *Ctenus* are relatively abundant, the density of adults is low during most of the year (Gasnier & Höfer 2001), and the density of *Phoneutria* is certainly much lower. Males of these genera in our study area probably have to search a great deal to find a receptive female. Selection for high mobility may be the reason for adult males with longer legs (shorter legs of juveniles and females may be more efficient for prey capture). Furthermore, high mobility in the leaf litter is probably more complicated for the smaller species, due to the relative size of the obstacles, which could cause a higher dimorphism in the relative size of the legs. Further studies will be necessary to verify if the pattern found for these species applies to other hunting spiders, specially for those foraging on the ground of forests, and to evaluate which are the selective pressures that determine different degrees of sexual dimorphism in hunting spiders.

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CHEMOSENSORY RESPONSE TO PREY IN *PHIDIPPUS AUDAX* (ARANEAE, SALTICIDAE) AND *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Many predators exploit the chemical signatures of prey when foraging. We present a comparative study designed to test if the foraging behavior of *Phidippus audax* (Hentz 1845) is manipulated by substrate-borne chemicals left by prey. Our findings suggest that foraging *P. audax* do not use chemical cues left by prey, while the wolf spider *Pardosa milvina* (Hentz 1844) in the same experimental setup does respond to chemical cues. However, further examination into the role of chemical cues on prey detection in salticids is required.

Keywords: Salticidae, Lycosidae, foraging, chemical cues

The sensory adaptations used to locate prey are diverse, varying with foraging strategy and elements of the environment (Cooper 2000). The ability to use chemical stimuli to detect prey has been found in both vertebrates (e.g., Burghardt 1973; Arnold 1981; Dittman et al. 1998; Nevitt 2000; Rangen et al. 2000) and invertebrates (e.g., Rebach 1996; Hori 1999, Mondor & Roitberg 2000) including spiders (Persons & Uetz 1996; Punzo & Kukoyi 1997; Persons & Rypstra 2000). Nevertheless, the use of chemical cues as a mechanism for detecting prey remains understudied in spiders and further investigation into its role is critical to our chances of understanding their foraging decisions.

We report a test of the hypothesis that *Phidippus audax* (Hentz 1845)(Araneae, Salticidae) uses chemical cues of prey to adjust its foraging behavior. The foraging behavior of ant-eating jumping spiders, *Habrocestum pulex* (Hentz 1846), has been found to be influenced by chemical cues from prey (Clark et al. 2000). However, it is assumed that this species is monophagous and, thus, may have a

heightened ability to respond to the chemical signature of its prey, while a generalist predator, such as *P. audax*, may not. Moreover, the cannibalistic jumping spider *Portia labiata* (Thorell 1887) appears to possess the ability to distinguish chemically between its own and conspecific egg sacs. Because this species is disposed to consume conspecific egg sacs, perhaps we may interpret this as chemical discrimination between prey (Clark & Jackson 1994).

Specifically, our aim was to examine the effects of substrate-borne chemical cues of prey on the amount of time invested in a given patch in *P. audax*. We compared our results (and tested our protocol) using the wolf spider *Pardosa milvina* (Hentz 1844)(Araneae, Lycosidae), because other wolf spiders have been demonstrated to respond to chemical prey cues on substrates (Persons & Uetz 1996; Persons & Rypstra 2000). *Phidippus audax* and *P. milvina* are excellent subjects to use in a comparative investigation as they are syntopic, cursorial, diurnally active, generalist predators, and employ both 'sit-and-wait' and 'active' foraging strategies (Givens 1978; Walker et al. 1999). However, because jump-

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ing spiders are renowned for their exceptional visual acuity, an intriguing contrast emerges that may separate them from other spiders in the nature of cues used in prey detection.

We captured all spiders (of both species) in the field in Amherst and Leverett, Massachusetts during the summer of 2000. All were kept in the laboratory for 2–6 weeks prior to testing. They were housed in plastic cages on a 13:11 light:dark cycle at approximately 26 °C. Once per week, we provided spiders with approximately five crickets (*Acheta domesticus*, Top Hat Cricket Farm, Kalamazoo, Michigan), which allowed spiders to feed to satiation. We provided water *ad libitum* in test tubes plugged with cotton. Prior to testing, spiders were starved for 10–15 days to ensure that they were hungry. Voucher specimens were deposited in the University of Massachusetts Department of Entomology insect collection.

Experiment 1, conducted on *P. audax* only, was a simultaneous choice test between two filter papers, one that had been exposed to crickets and one that had not. This protocol has been used previously in studies of wolf spider response to chemical prey cues (Persons & Uetz 1996, Persons & Rypstra 2000). We placed experimental filter papers (11 cm diameter) in petri dishes for 48–72 h with approximately 5–10 medium-sized juvenile crickets. Control papers were placed in petri dishes with no crickets.

The test arenas were clear plastic boxes (30 × 23 × 11 cm high). Between trials, the boxes were washed with soap, soaked in a diluted bleach solution for at least 10 min, rinsed, and wiped down with ethyl alcohol to reduce potential odor cues. The bottom of the box was divided into thirds. We randomly assigned treated and untreated filter papers to either side, leaving the middle neutral area open. To minimize potential visual disturbance, boxes were placed inside a large Rubbermaid® plastic storage bin (50 × 34 × 22 cm high) covered with opaque white paper.

Experiments were conducted in a quiet room during daylight hours under fluorescent light, between 22–25 °C. We placed each spider inside a large syringe with the top cut off and plugged the open end with a ball of tissue paper. The tip was placed through a hole in the side of the box near the center of the neutral area. We gave each spider a 5 min accli-

mation period in the syringe, and then removed the tissue paper and slowly pushed the syringe plunger to move the spider into the arena. Timing started as soon as the spider was released. Two digital timers were used to record the spider's activity. Because we were interested in whether spiders could detect cues when close to or touching the filter paper, we recorded both the time spent on each filter paper and the time spent in the third of the arena in which each paper was located. We observed each spider for 20 min. Each spider was given one trial.

It is possible that salticids may need to make physical contact with the substrate in order to detect chemical cues. However, spiders did not always sample both filter papers in experiment 1. We therefore designed experiment 2, a sequential presentation, where spiders were placed directly on a piece of filter paper that covered half of the bottom of the arena. We noted the time spent on or off the filter paper. We tested each spider twice, once with treated and once with untreated paper. The order of the presentation of filter papers was randomly assigned. In all other respects, this protocol was identical to experiment 1.

We tested 13 adult *P. audax* in experiment 1 and 15 in experiment 2, mostly females with several males in each test. We tested *P. milvina* only in experiment 2 ($n = 15$, 9 adult female, 6 adult male). Data were analyzed with Wilcoxon signed rank tests.

We found no evidence that *P. audax* distinguished between control and experimental filter papers. In experiment 1, there was no difference in the amount of time spiders spent on the untreated vs. the treated filter paper (Wilcoxon signed rank test, tied $Z = -0.105$, $p > 0.9$, $n = 13$, Fig. 1a). There was also no difference in the amount of time spiders spent in the third of the arena with the untreated paper vs. the third with the treated paper (Wilcoxon signed rank test, tied $Z = -0.549$, $p > 0.5$, $n = 13$). In experiment 2, we found no difference in the amount of time spiders spent on the control filter paper vs. the treated paper (Wilcoxon signed rank test, tied $Z = -0.369$, $p > 0.7$, $n = 15$, Fig. 1b). In contrast, *P. milvina* spent significantly more time on the treated filter paper than the untreated paper (Wilcoxon signed rank test, tied $Z = -3.237$, $p < 0.002$, Fig. 1c).

Pardosa milvina appear to possess chemo-

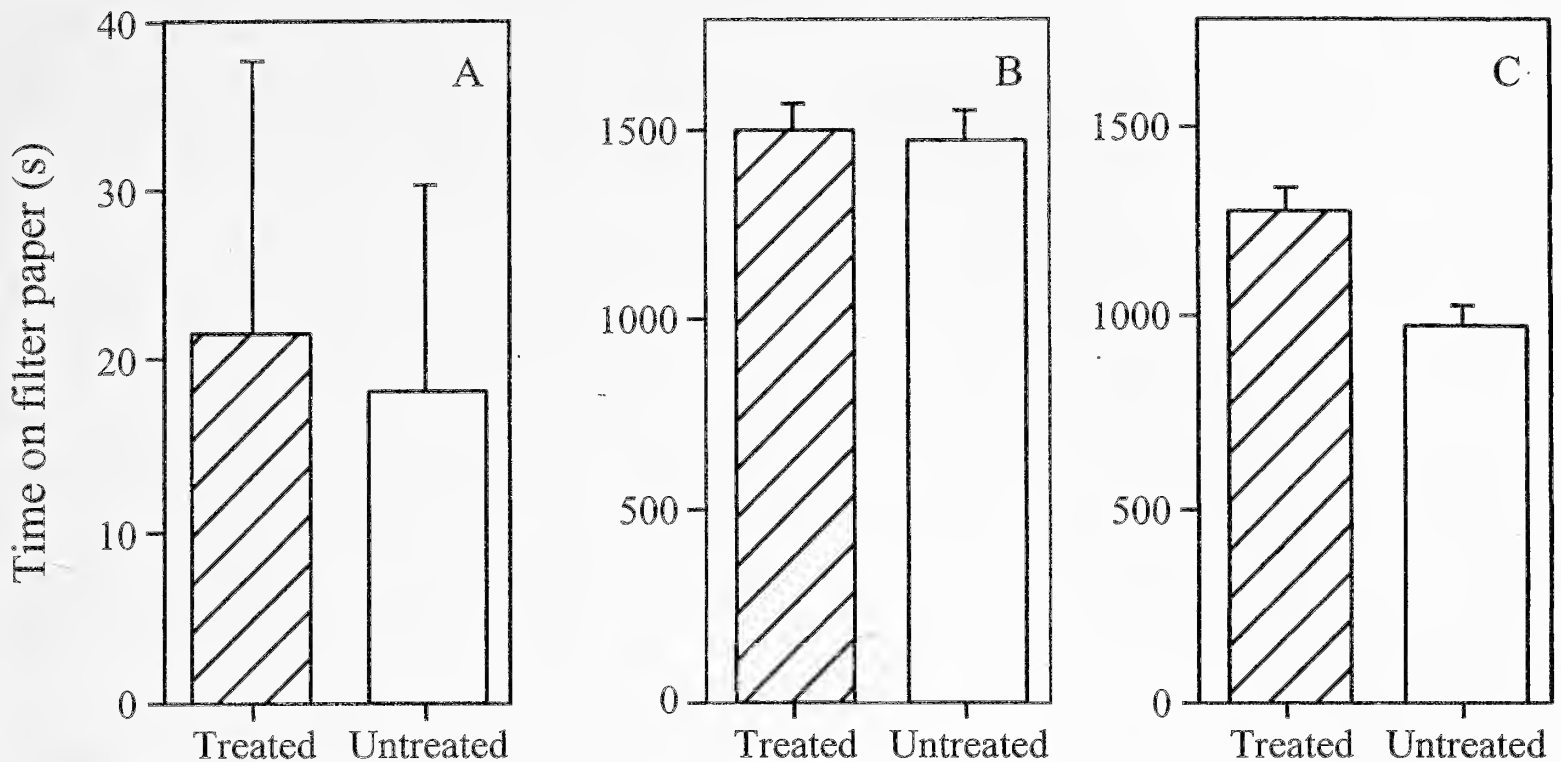


Figure 1.—The amount of time spent on cricket-treated vs. untreated filter paper. (A) Simultaneous presentation of both types of filter paper to *P. audax*. (B) Sequential presentation of both types of filter paper to *P. audax*. (C) Sequential presentation to *P. milvina*.

sensory ability. This finding is consistent with previous investigations of wolf spiders (Persons & Uetz 1996; Persons & Rypstra 2000). We frequently observed *P. milvina*, but not *P. audax*, passing their legs and palpal tarsi through the chelicerae as well as biting the edges of the cricket-treated filter paper substrata. We did not see these behaviors in trials with untreated filter paper substrata. This suggests that perhaps in addition to other chemical (e.g. olfactory) cues, gustatory cues may be important in the prey locating abilities of wolf spiders. However, we agree with the caution expressed by Persons & Uetz (1996) that because treated filter paper was exposed to large numbers of crickets over a period of days, the degree to which these spiders react to chemical cues of prey may be inflated in our study compared to natural situations.

Foraging patch residence times did not differ whether cricket-treated or untreated filter paper was used in *P. audax* trials. This is consistent with expectation if *P. audax* cannot or does not use chemical stimuli to locate prey. Jumping spiders depend strongly on visual cues of movement, size, and shape to capture prey (Land 1971; Dill 1975), and *P. audax* has been demonstrated to use species-specific visual cues to select and avoid potential prey (Freed 1984). Perhaps as a consequence of the evolution of exceptional visual faculties, che-

mosensory response to prey has abated. Some other highly visual species do not respond to chemical cues. For example, predatory water bugs *Microvelia macgregori* (Hemiptera, Veliidae) respond to visual and vibrational but not chemical cues during prey detection (Jackson & Walls 1998). Interestingly, lycosids also visually detect the movement of prey (e.g., Rovner 1993, Persons & Uetz 1998). This suggests that the difference we found between the species is not simply because *P. milvina* is incapable of visual prey detection.

At present, we are not prepared to suggest that *P. audax* lacks the ability to perceive chemical cues left by prey but that they do not react similarly to *P. milvina*. Perhaps *P. audax* perceives chemical cues of prey and subsequently responds by attempting to locate them visually as opposed to investing longer periods of time at the source engaging in overt gustatory or olfactory behaviors. It is important to note that *P. audax* does use chemical cues in the context of mating. For example, Oden (1981) demonstrated that adult male *P. audax* responds to chemical cues left by adult and sub-adult female conspecifics. Thus, we should be cautious not to prematurely reject any role for chemical cues in the context of foraging in *P. audax*, but this piece of evidence suggests that the role is less than for lycosids.

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HAWAIIAN SPIDERS OF THE GENUS *TETRAGNATHA*: IV NEW, SMALL SPECIES IN THE SPINY LEG CLADE

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ABSTRACT. This study continues documentation of the adaptive radiation of species in the genus *Tetragnatha* in the Hawaiian archipelago. The five new species described here are representatives of the ‘spiny-leg’ clade, most representatives of which have already been described. The new species are *T. kukuiki*, *T. kikokiko*, *T. anuenue*, *T. kukuhaa*, and *T. obscura*. The species described are found in various different habitat types from low (e.g., 550 m on Oahu) to middle elevations (1660 m on Hawaii), and from dry to very wet forest types. As with other representatives of the clade, they are nocturnal hunters, do not build webs, and move actively around the vegetation.

Keywords: Hawaii, *Tetragnatha*, spiny, descriptions

The Hawaiian island chain is the most isolated archipelago in the world, and as such is well known for having numerous autochthonous radiations of closely related species (Simon 1987; Wagner & Funk 1995; Roderick & Gillespie 1998). Groups of spiders that appear to have undergone extensive species radiations in the islands include *Tetragnatha* Latreille 1804 (Tetragnathidae) (Karsch 1880; Simon 1900; Okuma 1988; Gillespie 1991, 1992), *Mecaphesa* Simon 1900 (Thomisidae) (Simon 1900; Suman 1970; Lehtinen 1993; Garb 1999), *Argyroides* Simon 1864 (Theridiidae) (Simon 1900), *Theridion* Walckenaer 1805 (Theridiidae) (Simon 1900), and a lineage of jumping spiders (Salticidae) (Gillespie et al. 1998).

This paper is the fourth in a series documenting the radiation of *Tetragnatha* spiders in the archipelago. These species, in common with other endemic arthropods in Hawaii, are characterized by small population sizes (Howarth & Ramsay 1991). Also, in common with other adaptive radiations, they have differentiated rapidly (Gillespie 1999), and on the basis of ecological parameters (Gillespie et al. 2001). Because ecological affinity cannot be preserved, diagnosis must be based on a combination of sexual characters (cheliceral armature and genitalia). All sexual characters show some variation in most species of *Tetragnatha* (Levi 1981). Here, I will attempt to point out the diagnostic features of these structures within the range of variation.

The species described here are all small and do not build webs. Evidence from molecular characters (mitochondrial DNA) (Gillespie 1999) suggests that all five species belong within the now well-recognized ‘spiny-leg’ clade of Hawaiian *Tetragnatha* (12 described species, Simon 1900; Gillespie 1991). In addition, morphological and ecological characters unite these species with the spiny leg clade. These characters include long spines on the legs (similar to those found in species such as *T. laqueata* L. Koch 1872 from the western Pacific (Okuma 1980) and *T. viridis* Walckenaer 1841 from eastern North America (Levi 1981) although more robust in Hawaiian spiny leg species), and an active nocturnal foraging style without a web.

METHODS

Characters examined.—Morphological measurements taken were the same as those described in Gillespie (1991, 1992, 1994): arrangement of eyes (i.e. lens and associated visual pigment); cheliceral tooth pattern; form and setation of the first and third legs (I & III representing the greatest divergence in leg function); and form and pattern of the dorsum, venter, carapace and sternum. In order to estimate variability within a taxon and determine which features best characterize a species, where possible measurements were taken on six individuals of each sex of each species with additional observations on other individ-

Table 1.—Glossary of terms and abbreviations used in text, illustrated in Figs. 1, 2, 7, 80.

Term	Explanation
a	dorsal cheliceral spur (apophysis) used in locking female fang during mating
AX1	auxiliary guide tooth of lower row; small tubercle (may be absent or almost tooth-like) on distal retromargin of chelicerae
CITR	cheliceral inter-tooth ratio; ratio of 3 lengths: (1) between distal end of male chelicerae to sl; (2) sl to T; and (3) T to rsu1
Co, CoP	Conductor cap (Fig. 7, 80); Conductor cap projection (Fig. 80)
fl	setation on femur I
fIII	setation on femur III
G1	guide tooth of lower row; from distal end of chelicera retromargin of the chelicerae, first major tooth
Gu	small tubercle (may be absent or almost tooth-like) on distal promargin of chelicerae
L1-Ln	numbers of chelicera retromargin teeth in female, from distal end
L2	second tooth on chelicera retromargin in female, from distal end
L3	third tooth on chelicera retromargin in female, from distal end
mI	setation on metatarsus I
mIII	setation on metatarsus III
n/n/n	format for numbers of prolateral/dorsal/retrolateral macrosetae
rsu	remaining proximal teeth on promargin of chelicerae, besides sl and T
S1	from distal end of chelicera promargin, first major tooth on promargin
T	from distal end of chelicera promargin, second tooth, often quite large

uals once diagnostic characters had been identified. Genitalia of both sexes were examined using the methods described in Gillespie (1991).

Terminology.—The terminology for the teeth on the cheliceral margins of the males is that used in previous papers (Gillespie 1991, 1992, 1994; see Okuma 1987, 1988, see Table 1, Figs. 1, 2, 8). The majority of the speci-

mens were collected by me (RGG), A.C. Medeiros (ACM), C. Parrish (CP), W.D. Perreira (WDP), and D.J. Preston (DJP), and George Roderick (GKR). All holotypes have been deposited in the Bishop Museum, and all paratypes will be deposited in the Essig Museum of Entomology of the University of California, Berkeley. Unless indicated otherwise, all measurements are in mm.

KEY TO SPECIES

1. Males 2

Females 6
2. Conductor cap height greater than length of projection from cap; Figs. 78, 79; see Fig. 80 for terminology); leg spines not very distinctive; abdominal and cheliceral marking distinctive; legs distinctly banded 3

Conductor cap more wide than high (Figs. 77, 80–81); leg spines very distinctive; abdominal and cheliceral markings drab; legs not distinctly banded 4
3. Conductor cap angular (Fig. 79); dorsal tooth of chelicerae very long (approx. 20% length of carapace); spiders very colorful in life, with yellow background coloration and polymorphism in amounts of red, black superimposed (Fig. 37) *T. anuenue*

Conductor cap curved smoothly over (Fig. 78). Dorsal tooth of chelicerae quite short (approx. 12% length of carapace). Spiders not highly colored, patterns mostly of black/gray, white and dark red; no conspicuous color polymorphism *T. kikokiko*
4. Conductor cap very angular, bent round, with projection resembling beak of parrot (Fig. 77) *T. kukuiki*

Conductor cap not angular 5

5. Projection from cap of conductor drawn to smooth point (Fig. 80). Dorsal spur usually with shallow bifurcation (Fig. 49) *T. kukuhaa*
Projection from cap of conductor very long, curls over at tip (Fig. 81). Dorsal spur usually blunt (Fig. 64) *T. obscura*
6. Bulbs of seminal receptacles approximately at right angles to each other, the posterior lateral to the anterior bulb, forming a distinct “C” shape (Fig. 15) *T. kukuiki*
Bulbs of seminal receptacles approximately on the same plane 7
7. Either anterior or posterior bulb of seminal receptacles oval (Figs. 30, 46). Leg spines not very distinctive. Abdominal and cheliceral marking distinctive. Legs distinctly banded. Abdomen drawn up in dome-shaped, pointed at posterior 8
Bulbs of seminal receptacles subspherical (Figs. 61, 76). Leg spines distinctive. Abdomen not domed. Abdomen with distinct dark mark at center and rounded at posterior margin .. 9
8. Enlarged oval posterior bulb of seminal receptacles (Fig. 46). Medial side of tarsus I with 3/4 spines (Fig. 42); teeth on lower side of cheliceral margin spread out, tooth area covering approx. 35% length of chelicerae (Fig. 40); number of teeth on lower side of cheliceral margin > number on upper side; spiders very colorful in life, with yellow background coloration and variable amounts of red and black superimposed (Figs. 44, 45) ... *T. anuenue*
Enlarged oval anterior bulb of seminal receptacles (Fig. 30). Medial side of tarsus I with 1/2 spines (Fig. 26); teeth on lower side of cheliceral margin very close together, tooth area covering approx. 25% length of chelicerae (Fig. 24); number of teeth on lower side of cheliceral margin ≤ number on upper side; Spiders not highly colored, patterns mostly of black/gray, white and dark red; no conspicuous color variants (Figs. 28, 29) *T. kikokiko*
9. Anterior bulb of seminal receptacles larger, posterior bulb smaller and more lateral (Fig. 61). Leg spines very long (Fig. 57); lateral and medial eyes separated by almost their width (Fig. 56) *T. kukuhaa*
Bulbs of seminal receptacles paraxial, lateral slightly smaller than medial (Fig. 76). Leg spines not very long (Fig. 72); lateral and medial eyes separated by half their width (Fig. 71) *T. obscura*

Tetragnatha kukuiki new species
(Figs. 1–15, 77)

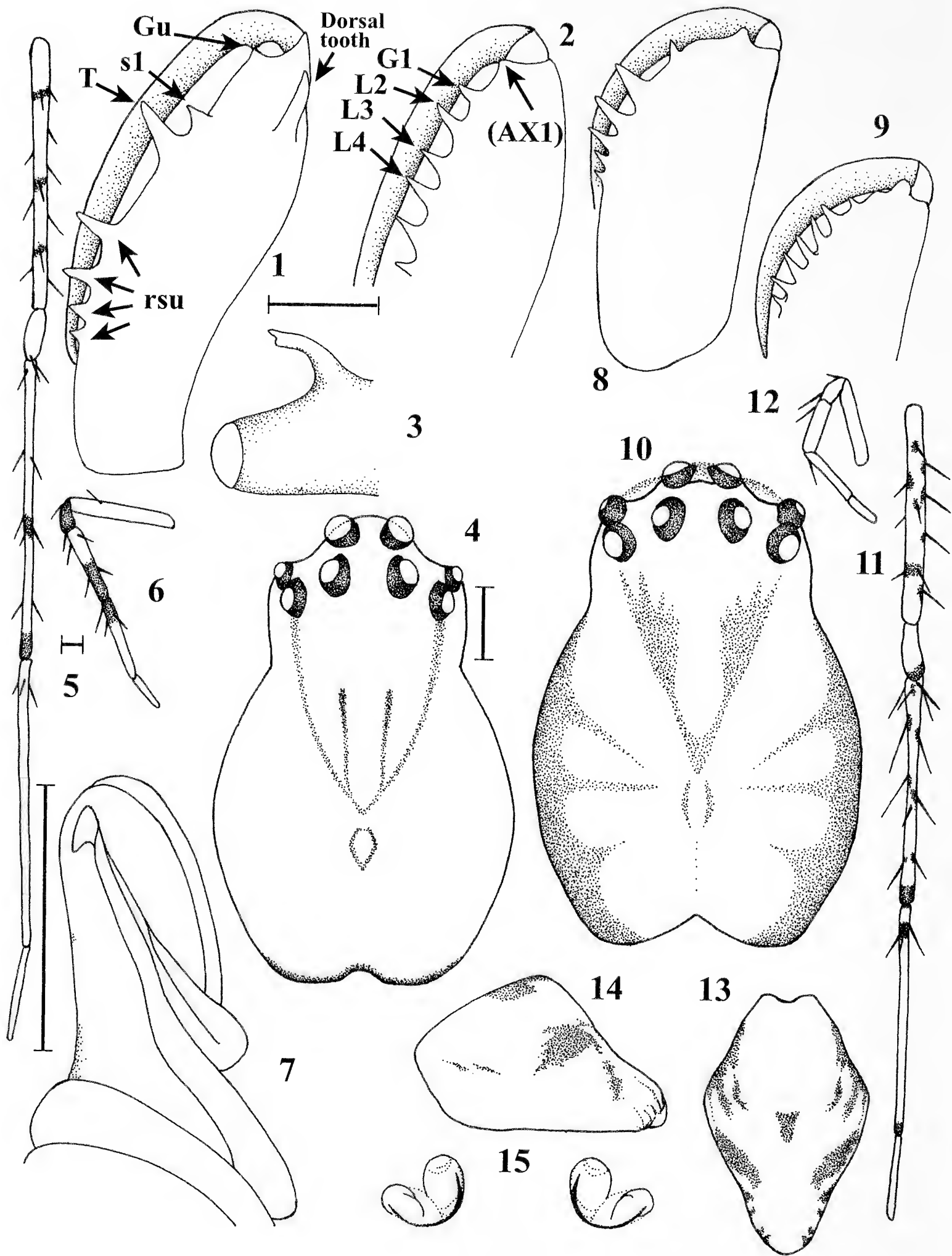
Type.—Holotype male from Oahu, Mt. Kaala, 550 m, coll. R.G. Gillespie and G.K. Roderick, 13 August 1995; allotype female from Oahu, Pahole, 600 m, coll. R.G. Gillespie and G.K. Roderick, 19 August 2000, deposited in the Bishop Museum, Honolulu.

Etymology.—*Kukū* (Hawaiian) spiny; *iki* (Hawaiian) small. The specific epithet is a noun in apposition. This species was the first of the “small spiny” species to be recognized, and hence was assigned this name.

Diagnosis.—*Tetragnatha kukuiki* can be confused with very small immature *T. quasimodo* Gillespie 1991, but is much smaller at maturity (total length approximately 4 compared to 6–8 in *T. quasimodo*). Male *T. kukuiki* are distinguished from all other spiny-leg taxa on the basis of the shape of the conductor cap (wide and angular).

Description.—*Holotype male* (Figs. 1–7): Length of carapace 1.6, total length 4.4. Chelicerae 1.0 (63% length of carapace). Chelic-

eral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 1): distance between Gu and s1 much greater than between s1 and T, CITR 0.4:0.2:0.4; Gu absent; s1 stout point bent slight towards base of chelicerae, width 40% length (approximately 41% width and 43% height of T); T tall peak (height 0.08) pointing out at a slight angle from margin of chelicerae; rsu 3–4 straight spikes. Retromargin of chelicerae (Fig. 2): total of 6 teeth; AX1 absent; G1 medium-sized, L2 larger; L3–L5 similar in size, L6 smaller. Dorsal spur quite long (length 0.32), curved over (20 % length of carapace); tip unequally bifurcate (Fig. 3). Coloration and eye pattern similar to female (Fig. 4). Legs banded below many of spines and at distal margins of leg segments (Figs. 5, 6). Leg setation: fl 3/3/5; tl 4/1/4; ml 1/1/1; flll 0/2/0, and tlll 2/2/2 and mlll 1/1/1. Leg spines not exceptionally long, mean length of spines on tl, 0.25. Conductor (Figs. 7, 77): conductor cap simple; not highly peaked, drawn out to point.



Figures 1–15.—*Tetragnatha kukuiki*; Male holotype. 1. Promargin of right chelicera; 2. Retromargin of left chelicera; 3. Dorsal spur of chelicera, lateral view; 4. carapace, dorsal; 5. Right leg I, dorsal; 6. Right leg III, prolateral; 7. Left palp. Female allotype. 8. Promargin of right chelicera; 9. Retromargin of left chelicera; 10. Carapace, dorsal; 11. Right leg I, dorsal; 12. Right leg III, prolateral; 13. Abdomen, dorsal; 14. Abdomen, lateral; 15. Seminal receptacles, ventral. Scale bars = 0.5; that at Fig. 1 applies to Figs. 1–3; at Fig. 4 to Fig. 4; at Fig. 5 to Figs. 5, 6; at Fig. 7 to Fig. 7, and at Fig. 8 to Fig. 8. For abbreviations, see glossary, Table 1.

Allotype female (Figs. 8–15): Length of carapace 1.5, total length 4.8. Chelicerae slightly less than half length of carapace. Cheliceral fang just over half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 8): 6 teeth, U1 short (length 0.03), much narrower and shorter (35%) than U2, separated from U2 by 14% cheliceral length; U2 fairly large, 0.10; U3 of similar height, U4–U6 decreasing in size proximally. Retromargin of chelicerae (Fig. 9): series of 7 teeth: L1 slightly smaller than U1, 50% height and fairly well separated from L2. Remaining retromarginal teeth decreasing in size proximally. Eyes slightly larger than distance separating them. Median ocular area slightly wider posteriorly (Fig. 10); lateral eyes contiguous. Carapace pale brown with dark margins, and additional dark marks converging on thoracic fovea; sternum dusky. Abdomen raised to a peak, height 2.0; dorsum marked with black on pale brown background (Figs. 13–14); venter speckled silver with brown medial, longitudinal bar. Legs with pronounced spots below spines, and at distal margins of each joint (Figs. 11–12). Leg setation: fl 2/3/2; tl 4/2/4; mI 1/1/1; fIII 0/0/0, tIII 0/1/0 and mIII 0/1/0. Leg spines long, mean length of spines on tl, 0.59. Seminal receptacles (Fig. 15): Posterior bulb lateral to anterior bulb, slightly smaller than anterior; both elongate oval in shape.

Variation.—($n = 2\sigma, 4\varphi$) *Male*: Carapace 1.4–1.8. CTR no variation, 0.4:0.2:0.4. Up to 8 teeth on retromargin of chelicerae. Tip of dorsal spur can be equally bifurcate. Color patterns vary slightly; no polymorphism. *Female*: Length of carapace 1.4–1.7. Promargin of chelicerae: series of 6–7 teeth. Leg setation: fl variable numbers of setae.

Natural history.—*Tetragnatha kukuiki* is found in low elevation mesic forest on Oahu. This forest is currently dominated by alien vegetation, primarily strawberry guava and eucalyptus. The specimens were found actively moving around in the branches of the trees.

Paratypes.—Oahu, Mt. Kaala, 550 m, RGG and GKR, 13 August 1995, 1 male; Oahu, Pahole, 600 m, JE Garb, 20 May 1999, 1 male. Oahu, Pahole, 600 m, RGG and GKR, 19 August 2000, 4 females.

Tetragnatha kikokiko new species
(Figs. 16–30, 78)

Types.—Holotype male, allotype female from Maui, Auwahi, 1250 m, coll. R.G. Gil-

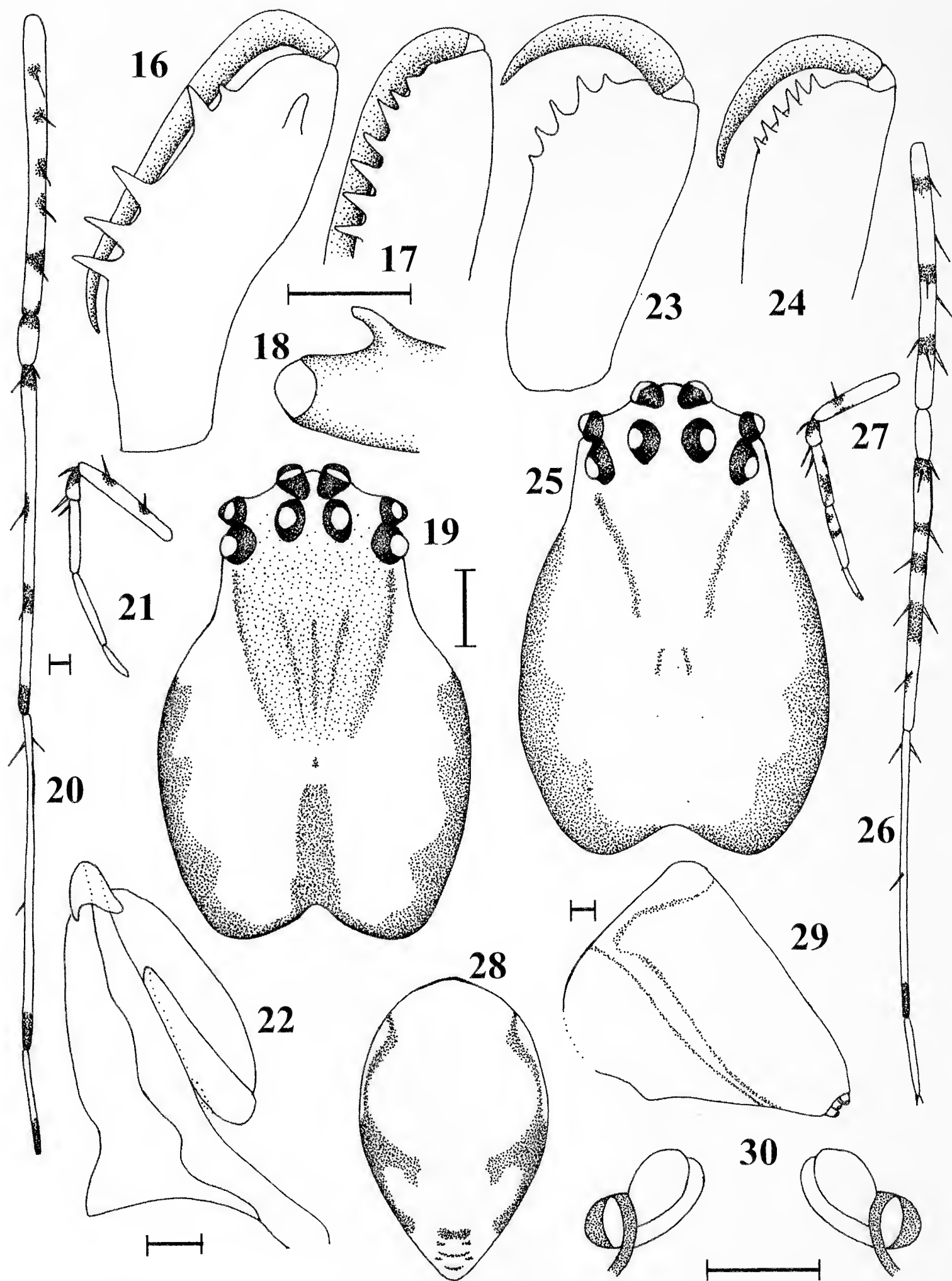
lespie and A.C. Medeiros, 18 August 1997, deposited in the Bishop Museum, Honolulu.

Etymology.—*Kikokiko* (Hawaiian) spotted or banded; refers to the very conspicuous banded legs of these small spiders. The specific epithet is a noun in apposition.

Diagnosis.—*Tetragnatha kikokiko* is most easily confused with *T. restricta* Simon 1900 and small immature *T. quasimodo*. Compared to *T. quasimodo*, *T. kikokiko* is much smaller in size at maturity (female length 3.5–4.5 compared to 6–8 in *T. quasimodo*), the eyes are larger and closer together, and the spines shorter. The abdomen is pointed (not raised up along a medial flat line across abdomen as in *T. restricta*) and without a prominent central black mark (as in *T. quasimodo*). It can also be distinguished from all other spiny-leg taxa by the shape of the conductor cap (high and smoothly curved).

Description.—*Holotype male* (Figs. 16–22): Length of carapace 1.4, total length 3.6. Chelicerae 0.8 (57% length of carapace). Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 16): distance between Gu and s1 much greater than between s1 and T, CTR approx. 0.4:0.2:0.4, reflecting close proximity of s1 and T and large separation of T from rsu; Gu indistinct or absent; s1 prominent point, width about half length (approximately 70% width and 45% height of T); T not very large (height 0.05) or wide, pointing straight out from margin of chelicerae; rsu 3 straight spikes, first few similar in size or even larger, than T. Retromargin of chelicerae (Fig. 17): total of 7 teeth; AX1 absent or indistinct; G1 small, L2–L7 showing slight increase in size proximally. Dorsal spur quite short (length 0.15), bent (11 % length of carapace); tip flat-faced (Fig. 18). Thoracic fovea indistinct “V”-shaped depression. Coloration and eye pattern as in female (Fig. 19). Abdomen less elevated than female. Leg setation similar to female (Figs. 20, 21). Conductor (Figs. 22, 78): conductor cap quite broad and not highly peaked, drawn out to point; stem curved over to form short flange projecting behind cap.

Allotype female (Figs. 23–30): Length of carapace 1.3, total length 3.8. Chelicerae just less than half length of carapace. Cheliceral fang quite short (approximately half length of base), tapering to smooth point distally. Pro-



Figures 16–30.—*Tetragnatha kikokiko*; Male holotype. 16. Promargin of right chelicera; 17. Retromargin of left chelicera; 18. Dorsal spur of chelicera, lateral view; 19. carapace, dorsal; 20. Right leg I, dorsal; 21. Right leg III, prolateral; 22. Left palpus, prolateral. Female allotype. 23. Promargin of right chelicera; 24. Retromargin of left chelicera; 25. Carapace, dorsal; 26. Right leg I, dorsal; 27. Right leg III, prolateral; 28. Abdomen, dorsal; 29. Abdomen, lateral; 30. Seminal receptacles, ventral. Scale bars for Figs. 16–21 and 23–29, 0.5; scale bars for Figs. 22 & 30, 0.1. That at Fig. 18 applies to Figs. 16–18, 23, 24; at Fig. 19 to Figs. 19, 25; at Fig. 20 to Figs. 20, 21, 26, 27; at Fig. 29 to Figs. 28, 29; and Fig. 22 to Fig. 22; and Fig. 30 to Fig. 30.

margin of chelicerae (Fig. 23): 5 teeth, U1 short (length 0.02), almost as wide but shorter (60%) and close to (9% cheliceral length) U2 and U3; U2 not large, 0.04; U3 of similar height, U4–U5 decreasing in size proximally. Retromargin of chelicerae (Fig. 24): series of 6 teeth: L1 taller than U1, similar in size and very close to L2. Remaining retromarginal teeth decreasing in size proximally. Eyes larger than distance separating them. Median ocular area slightly wider posteriorly (Fig. 25); lateral eyes contiguous. Carapace brown with dark margins, and pair of dark lines running from behind PLE's and converging broadly towards fovea; sternum dusky. Abdomen raised towards medial point, height 2.1; dorsum brown with dark margins, converging towards posterior (Figs. 28, 29); venter speckled silver with brown medial, longitudinal bar. Legs with large dark spots or bands below each spine and at distal margins of each joint (Figs. 26, 27. Leg setation: fl 0/3/2; tI 2/2/2; mI 1/0/1; fIII 0/1/0, tIII 0/1/0 and mIII 0/0/0. Leg spines not exceptionally long, mean length of spines on tI, 0.28. Seminal receptacles (Fig. 30): enlarged oval anterior bulb; smaller, more lateral, posterior bulb.

Variation.—($n = 6\delta, 6\eta$) Male: Carapace 1.2–1.5. CITR little variation, 0.4:0.2:0.4; rsu up to 4. Tip of dorsal spur can be slightly indented. Female: Length of carapace 1.2–1.5. Promargin of chelicerae up to 7 teeth. Color patterns vary slightly; no polymorphism. Leg setation similar within Auwahi, but in Waikamoi: fl 1/3/4; tI 3/1/2; other setation patterns similar.

Natural history.—*Tetragnatha kikokiko* is found in dry and mesic forest at middle elevations on East Maui. Populations have been found in remnant dry forest of Auwahi on the south slope of East Maui, a small dryland community on unweathered lava with little soil formation. It is also found in mesic forest on the north slope of East Maui at the western side of the Nature Conservancy of Hawaii's Waikamoi Preserve. Individuals do not build webs. They are found actively moving about and hanging from trees at night.

Paratypes.—Maui Island, Auwahi tract: 1100–1250 m, RGG & ACM, 18 August 1997, 2 δ , 3 η . Maui Island, Waikamoi: 1340 m, RGG, 9 November 1996, 2 δ , 4 η ; same area, RGG & ACM, 27 July 1999, 2 δ , 2 η .

Tetragnatha anuenue new species
(Figs. 31–46, 79)

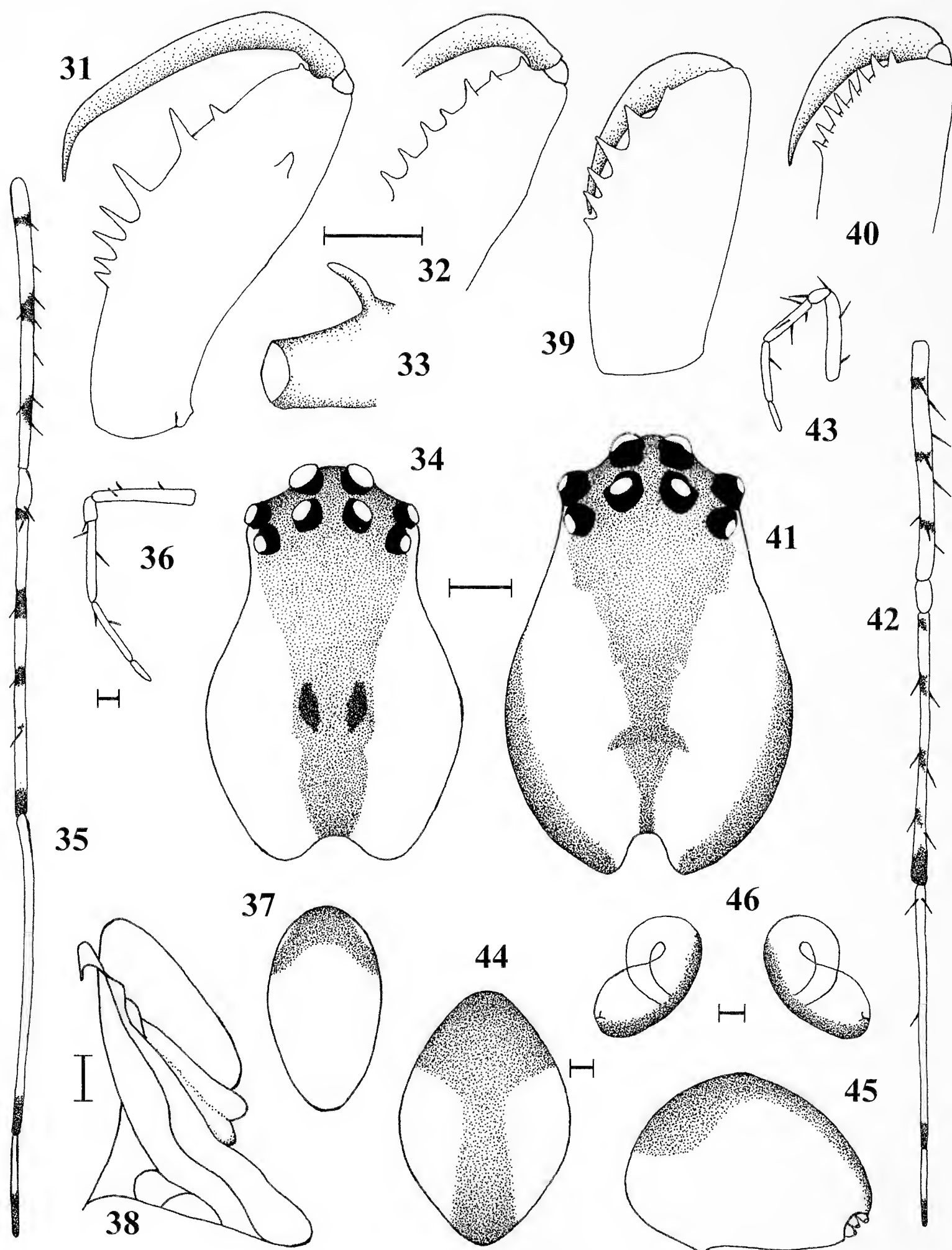
Types.—Holotype male from Hawaii Island, Saddle Road, 1530 m, coll. R.G. Gillespie, 12 June 1989; allotype female from Hawaii Island, Puu Makaala, 1215 m, coll. R.G. Gillespie, 14 October 1990; deposited in the Bishop Museum, Honolulu.

Etymology.—*Anuenue* (Hawaiian) rainbow. This refers to the colorful nature of these spiders, with many different bright color morphs. The specific epithet is a noun in apposition.

Diagnosis.—*Tetragnatha anuenue* is not easily confused with other species. The animal is generally strikingly patterned, with variable amounts of red or black pigment superimposed on a pale translucent yellow/gold background. It can also be distinguished on the basis of the shape of the conductor cap (high and angular), long dorsal spur, and the female seminal receptacles (enlarged oval posterior bulb).

Description.—*Holotype male* (Figs. 31–38): Length of carapace 1.5, total length 3.8. Chelicerae 1.0 (70% length of carapace). Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 31): distance between Gu and s1 much greater than between s1 and T, CITR 0.5:0.2:0.3; Gu indistinct or absent; s1 small point, width 42% length (approximately 60% width and 33% height of T); T tall spike (height 0.07) pointing directly out from margin of chelicerae; rsu 5 straight spikes. Retromargin of chelicerae (Fig. 32): total of 6 teeth; AX1 absent or indistinct; G1 small and wide, L2 taller and wider; rest of teeth narrower spikes, L4–L6 similar in height to L2 (L3 shorter). Dorsal spur long (length 0.27), with strong, angular bend (18 % length of carapace); tip pointed (Fig. 33). Thoracic fovea indistinct depression. Dorsum coloration pale yellow/gold with red “U” shape at front (Fig. 37). Eye pattern (Fig. 34) and leg setation (Figs. 35–36) similar to female. Conductor (Figs. 38, 79): conductor cap simple, highly peaked.

Allotype female (Figs. 39–46): Length of carapace 1.6, total length 4.3. Chelicerae approx. half length of carapace. Cheliceral fang just over half length of base, tapering to smooth point distally. Promargin of chelicerae



Figures 31–46.—*Tetragnatha anuenue*; Male holotype. 31. Promargin of right chelicera; 32. Retro-marginal teeth of left chelicera; 33. Dorsal spur of chelicera, lateral view; 34. carapace, dorsal; 35. Right leg I, dorsal; 36. Right leg III, prolateral; 37. Abdomen, dorsal (stippling indicates red coloration); 38. Left palpus, prolateral. Female allotype. 39. Promargin of right chelicera; 40. Retro-marginal teeth of left chelicera; 41. Carapace, dorsal; 42. Right leg I, dorsal; 43. Right leg III, prolateral; 44. Abdomen (stippling indicates red coloration), dorsal; 45. Abdomen, lateral; 46. Seminal receptacles, ventral. Scale bars for Figs. 31–37 & 39–45, 0.5; scale bars for Figs. 38 & 46, 0.1. That at Fig. 33 applies to Figs. 31–33, 39, 40; at Fig. 34 to Figs. 34, 41; at Fig. 35 to Figs. 35, 36, 42, 43; at Fig. 44 to Figs. 37, 44, 45; at Fig. 38 to Fig. 38; and at Fig. 46 to Fig. 46.

(Fig. 39): 6 teeth, U1 short (length 0.03), almost as wide but much shorter (30%) than U2, separated from U2 by 15% cheliceral length; U2 fairly large, 0.09; U3 of similar height, U4–U6 decreasing in size proximally. Retromargin of chelicerae (Fig. 40): series of 8 teeth: L1 approx. same size as U1, 60% height and fairly close to L2. Remaining retromarginal teeth decreasing in size proximally. Eyes considerably larger than distance separating them. Median ocular area slightly wider posteriorly (Fig. 41); lateral eyes contiguous. Carapace pale yellow with dark margins, and dark medial area constricted behind thoracic fovea; sternum dusky. Abdomen smoothly domed, height 1.7; dorsum with red markings on pale speckled gold background (Figs. 44, 45); venter speckled silver with brown medial, longitudinal bar. Legs banded below many spines, and at distal margins of each joint (Fig. 42). Leg setation: fl 1/4/5; tl 3/2/4; ml 2/0/1; fIII 0/2/0, tIII 1/1/1 and mIII 0/0/1. Leg spines not notably long, mean length of spines on tl, 0.39. Seminal receptacles (Fig. 46): Enlarged elongate oval posterior bulb; smaller, more medial, anterior bulb.

Variation.—($n = 6\sigma$, 6φ) *Male*: Carapace 1.5–1.9. CTR little variation. 0.5:0.2:0.3; rsu 4–5. Retromargin of chelicerae 6–8 teeth. *Female*: Length of carapace 1.4–1.8. Carapace variable pale yellow or brown with dark margins, and variable dark medial. Highly polymorphic markings of black, brown and red, on speckled gold background of dorsum. Banding on legs of variable intensity. Leg setation: fl variable; tl 3/1/3; ml 2/0/1; fIII sometimes 2 dorsal.

Natural history.—*Tetragnatha anuenue* is found in middle elevation wet forest on Hawaii Island. It is a beautiful animal in life, exhibiting striking color polymorphism of red and black patterns superimposed on a yellow background (Figs. 37, 44, 45 depict 2 patterns, although the colors fade in alcohol). Individuals do not build webs and are generally found hanging from trees at night.

Paratypes.—Hawaii Island, Mauna Kea–Mauna Loa Saddle: Kipuka 6–8, Saddle Road, 1540–1600 m, RGG & CP, 25 July 1988, 3 σ , 4 φ , and RGG, 12 June 1989, 2 φ , and RGG & CP, 11 January 1991, 1 φ ; Kipuka 9, Saddle Road, 1530 m, RGG & CP, 4 January 1991, 10 σ , 8 φ , and WDP, 1 April 1991, 1 φ ; Kipuka at mile 21–22, 1660 m, RGG & JI Gillespie,

12 March 1990, 1 φ ; Wailuku River, 1067 m, RGG & CP, 12 July 1988, 1 φ ; Kipuka, Saddle Road, 823 m, RGG & CP, 25 July 1988, 1 σ ; Puu Makaala, 1222 m, RGG and JI Gillespie, 17 March 1990, 2 φ , 1 σ ; and RGG, DJP, and I Felger 14 October 1990, 7 φ , 6 σ , and RGG and CP, 3 January 1991, 3 φ , and RGG, 29 July 1991, 1 φ , 2 σ ; and 4300ft, RGG, DJP, and I Felger, 21 October 1990, 1 σ , 4 φ ; Lapaohoe, 1257 m (1 φ , 1 σ), 976 m (1 φ), and 700m (1 φ), 19 October 1990, RGG, DJP, & J. Burgett.

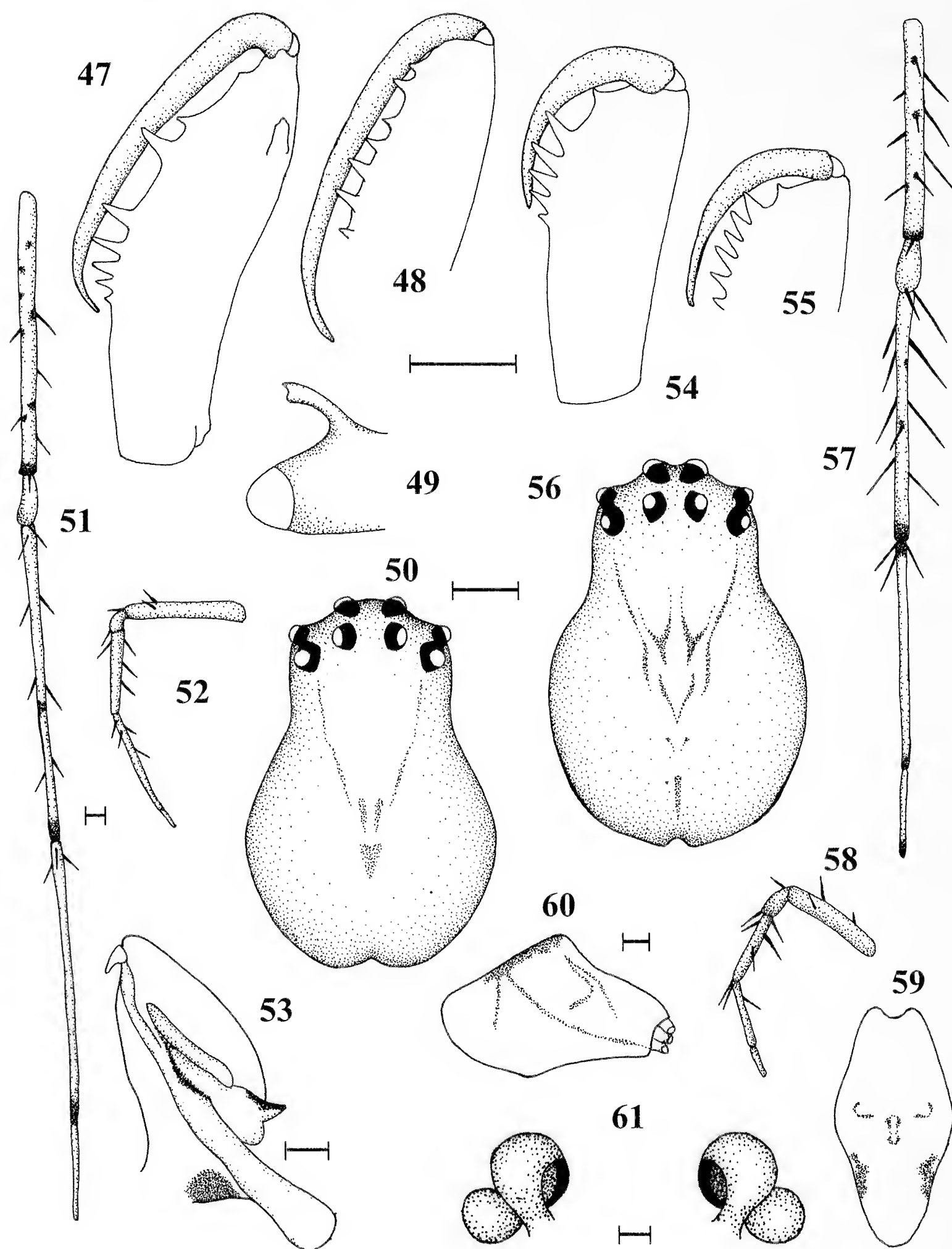
***Tetragnatha kukuhaa* new species**
(Figs. 47–61, 80)

Types.—Holotype male, allotype female from Hawaii Island, Puu Waawaa, 1215 m, coll. R.G. Gillespie and J. Giffin, 12 February 1997, deposited in the Bishop Museum, Honolulu.

Etymology.—*Kukū* (Hawaiian) spiny; *ha'a* (Hawaiian) dwarf. The specific epithet is a noun in apposition.

Diagnosis.—*Tetragnatha kukuhaa* is most easily confused with *T. restricta* and small immature *T. quasimodo*. Compared to *T. quasimodo*, it is smaller in size at maturity (female length 5 compared to 6–8 in *T. quasimodo*). The abdomen is pointed (not raised up along a medial flat line across abdomen as in *T. restricta*). Other features that distinguish the species from all other spiny-leg taxa include the cheliceral dentition and the shape of the conductor cap (wide with projection drawn to a smooth point) and seminal receptacles (bulbs subspherical, anterior bulb larger).

Description.—*Holotype male* (Figs. 47–53): Length of carapace 1.9, total length 4.8. Chelicerae 1.4 (75% length of carapace). Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 47): distance between Gu and s1 twice as much or more than distance between s1 and T, CTR 0.5:0.2:0.3; Gu indistinct or absent; s1 fairly prominent point, projecting from margin at a slight angle towards the base of the chelicerae, width approx. 40% length (approx. 40% width and height of T); T large (height 0.09), robust peak; rsu 5 almost straight spikes. Retromargin of chelicerae (Fig. 48): total of 7 teeth; AX1 absent or indistinct; G1 similar in size to L3 and both are much shorter than remain-



Figures 47–61.—*Tetragnatha kukuhaa*; Male holotype. 47. Promargin of right chelicera; 48. Retromargin of left chelicera; 49. Dorsal spur of chelicera, lateral view; 50. carapace, dorsal; 51. Right leg I, dorsal; 52. Right leg III, prolateral; 53. Left palpus, prolateral. Female allotype. 54. Promargin of right chelicera; 55. Retromargin of left chelicera; 56. Carapace, dorsal; 57. Right leg I, dorsal; 58. Right leg III, prolateral; 59. Abdomen, dorsal; 60. Abdomen, lateral; 61. Seminal receptacles, ventral. Scale bars for Figs. 47–52 & 54–60, 0.5; scale bars for Figs. 53 & 61, 0.1. That at Fig. 54 applies to Figs. 47–49, 54, 55; at Fig. 50 to Figs 50, 56; at Fig. 51 to Figs. 51, 52, 57, 58; at Fig. 60 to Figs. 59, 60; at Fig. 53 to Fig. 53; and at Fig. 61 to Fig. 61.

ing retromarginal teeth; L2, L4, L5 and L6 all large spikes. Dorsal spur long (0.38, approx. 20% carapace length), tip bifurcated (Fig. 49). Thoracic fovea indistinct "V" shape. Coloration and eye pattern as in female. Leg setation similar to female (Figs. 51, 52). Conductor (Figs. 53, 80): conductor cap simple, not highly peaked; apex pointed.

Allotype female (Figs. 54–61): Length of carapace 2.0, total length 5.1. Chelicerae just more than half length of carapace. Cheliceral fang approx. half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 54): series of 6 teeth; U1 robust (length 0.04), much shorter (30%) and well separated from (18 % cheliceral length) U2 and U3; U2 large, length 0.13, and U3 only very slightly shorter; U4–U6 decreasing in size proximally. Retromargin of chelicerae (Fig. 55): series of 6 teeth decreasing in size proximally: L1 similar in height to U1, about 30% height of L2 and well separated from L2. Eyes approx. same size as distance separating them; median ocular area wider posteriorly (Fig. 56); lateral eyes contiguous. Carapace brown with "V"-shaped fovea; sternum dusky. Abdomen raised to low peak at midline, height 1.7; dorsum brown with black marks in front and behind wider and higher medial area (Figs. 59, 60); venter speckled silver with brown medial, longitudinal bar. Legs brown with dark spots around femoral spines and dark bands at distal margins of each joint (Figs. 57, 58). Leg setation: fl 3/3/3; tl 4/1/4; ml 1/1/1; fIII 0/2/1, tIII 1/1/1 and mIII 0/1/1. Leg spines long, mean length of spines on tl, 0.95. Seminal receptacles (Fig. 61): anterior bulb larger, posterior bulb smaller and more lateral.

Variation.—($n = 3 \delta, 3 \text{♀}$) *Male*: Carapace 1.7–2.0. CTR can be 0.4:0.2:0.4; rsu 4–5. Retromargin of chelicerae 6–7 teeth. *Female*: Length of carapace 1.8–2.1. Promargin of chelicerae: series of 5–7 teeth. Leg setation: fl may be 3/3/5; tIII sometimes 2 prolateral macrosetae.

Natural history.—*Tetragnatha kukuhaa* has only been collected in the dry forest of Puu Waawaa, where it is found moving among, and hanging from, branches of trees.

Paratypes.—Hawaii Island, Puu Waawaa 1040 m, RGG, 12 February 1997, 2 δ , 2 ♀ .

Tetragnatha obscura new species
(Figs. 62–76, 81)

Types.—Holotype male, allotype female from Hawaii Island, Kahaualea, 515 m, coll.

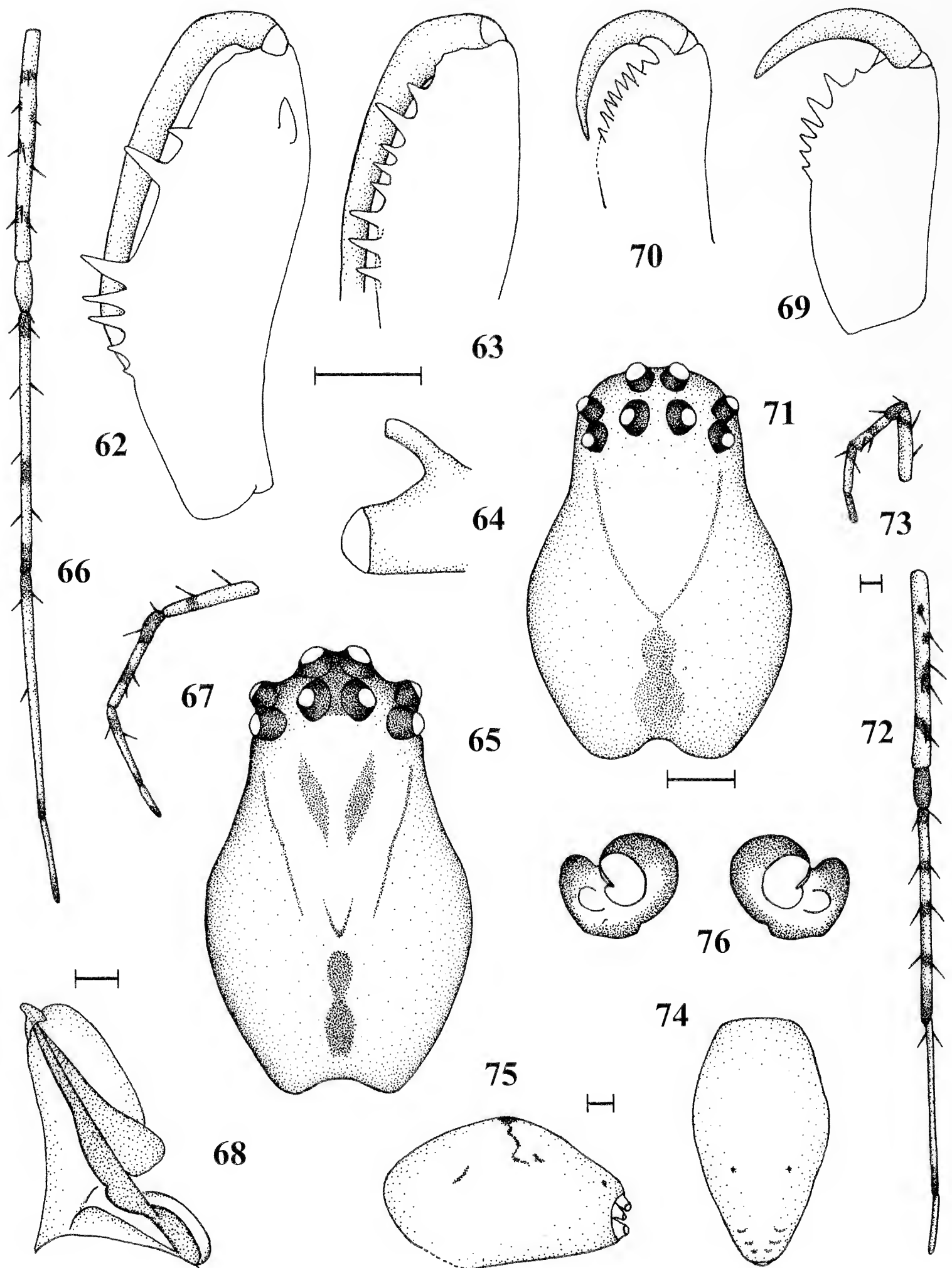
R.G. Gillespie, 2 January 1991, deposited in the Bishop Museum, Honolulu.

Etymology.—*Obscurus* (Latin) obscure or inconspicuous. The specific epithet is an adjective and refers to the small size and brown coloration of these spiders, which combine to make them rather inconspicuous.

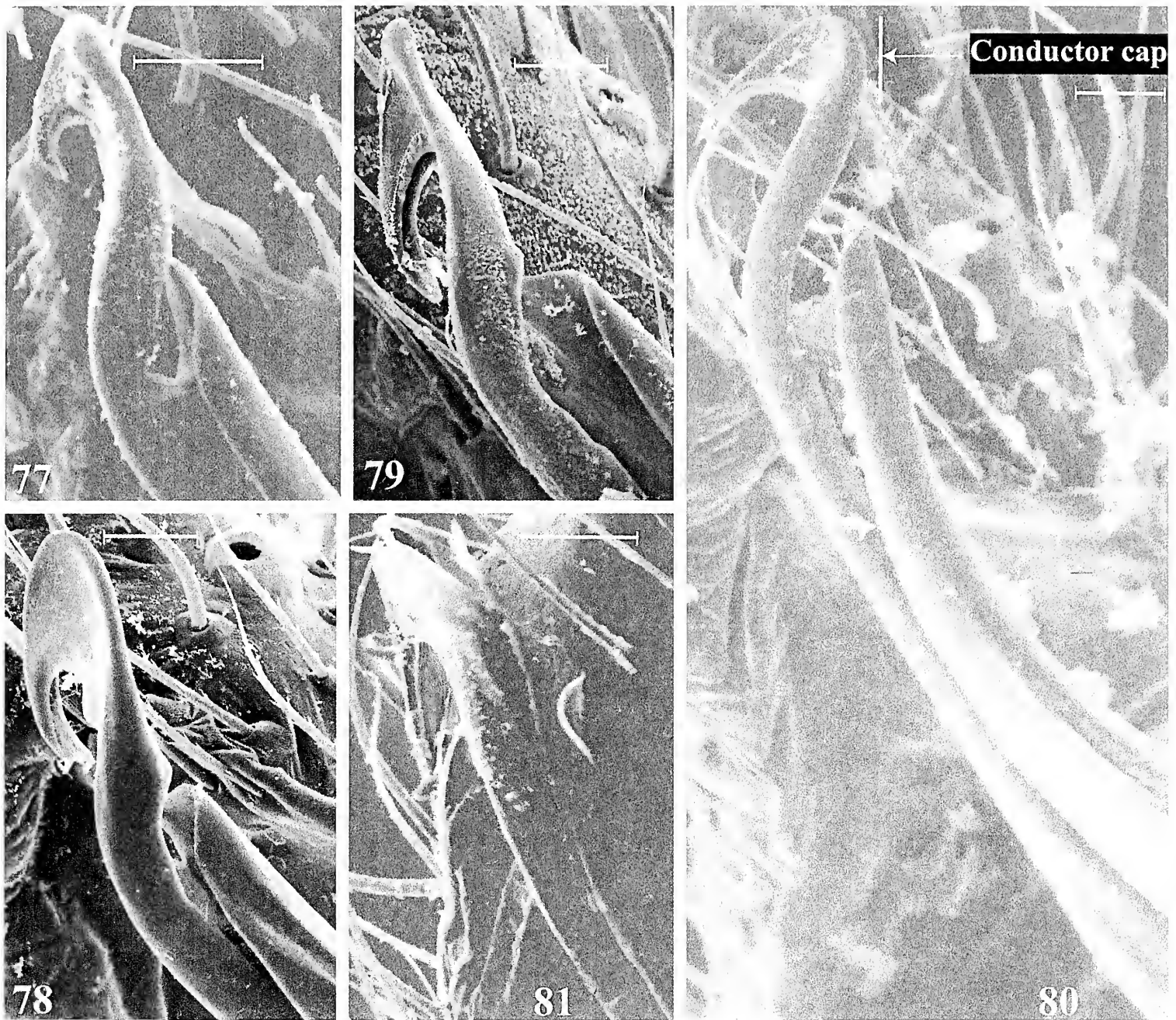
Diagnosis.—*Tetragnatha obscura* is most similar to small *T. quasimodo*, but is smaller in size (approximate female length 4 compared to 6–8 in *T. quasimodo*), the abdomen is not raised to a medial peak, and the eyes are relatively larger and closer together. Other features that distinguish it from all other spiny-leg taxa include the cheliceral dentition and the shape of the conductor cap and seminal receptacles.

Description.—*Holotype male* (Figs. 62–68): Length of carapace 1.6, total length 3.9. Chelicerae 70% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 62): distance between Gu and s1 much greater than between s1 and T, CTR 0.4:0.2:0.4; Gu indistinct or absent; s1 fairly prominent point, projecting straight out from margin of chelicerae, width approx. 44% length (approx. 70% width and 40% height of T); T large (height 0.07), robust point; rsu 5 almost straight spikes. Retromargin of chelicerae (Fig. 63): total of 8 teeth; AX1 absent or indistinct; G1 a robust spike, similar in height but wider than L3–L8. L2 long, almost twice as long as any of other retromarginal teeth. L3–L8 show slight increase in size proximally. Dorsal spur medium length (length 0.26, approx. 16 % carapace length), almost straight, and with blunt tip that may show slight bifurcation (Fig. 64). Thoracic fovea longitudinal depression. Coloration and eye pattern as in female. Leg setation similar to female (Figs. 66, 67). Conductor (Figs. 68, 81): conductor cap simple; apex pointed.

Allotype female (Figs. 69–76): Length of carapace 1.4, total length 3.7. Chelicerae just less than half length of carapace. Cheliceral fang approx. half length of base. Promargin of chelicerae (Fig. 69): series of 7 teeth; U1 robust (length 0.03), shorter (40%) and close to (10 % cheliceral length) U2 and U3; length of U2 0.07, U3 only very slightly shorter; U4–U6 decreasing in size proximally. Retromargin of chelicerae (Fig. 70): series of 8 teeth



Figures 62–76.—*Tetragnatha obscura*; Male holotype. 62. Promargin of right chelicera; 63. Retromargin of left chelicera; 64. Dorsal spur of chelicera, lateral view; 65. carapace, dorsal; 66. Right leg I, dorsal; 67. Right leg III, prolateral; 68. Left palpus, prolateral. Female allotype. 69. Promargin of right chelicera; 70. Retromargin of left chelicera; 71. Carapace, dorsal; 72. Right leg I, dorsal; 73. Right leg III, prolateral; 74. Abdomen, dorsal; 75. Abdomen, lateral; 76. Seminal receptacles, ventral. Scale bars for Figs. 62–67 & 69–75, 0.5; scale bars for Figs. 68 & 76, 0.1. That at Fig. 63 applies to Figs. 62–64, 69, 70; at Fig. 71 to Figs. 65, 71; at Fig. 72 to Figs. 66, 67, 72, 73; at Fig. 75 to Figs. 74, 75; at Fig. 68 to Figs. 68, 76.



Figures 77–81.—Scanning electron micrographs of conductor tips of male palps (scale bar on each represents 20 μm): 77. *T. kukuiki*; 78. *T. kikokiko*; 79. *T. anuenue*; 80. *T. kukuhaa*; 81. *T. obscura*; Co, Conductor cap; CoP, Conductor cap projection.

decreasing in size proximally: L1 similar in height to U1, about 40% height of L2 and almost contiguous with L2. Eyes considerably larger than distance separating them; median ocular area slightly wider posteriorly (Fig. 71); lateral eyes contiguous. Carapace brown with dark margins, dark lines converging from behind posterior lateral eyes to thoracic fovea. Thoracic fovea wide longitudinal bar; sternum dusky. Abdomen raised very slightly to low peak at midline, height 1.4; dorsum brown with medial black mark and paired lateral black marks just in front and behind the midline, and paired chevron marks at posterior (Figs. 74, 75); venter speckled silver with brown medial, longitudinal bar. Legs brown with dark spots around spines and dark bands at distal margins of tibia, metatarsus and tarsus (Figs. 72, 73). Leg setation: fl 0/3/3; tl 2/

2/1; mI 1/0/1; fIII 0/2/0, tIII 0/0/1 and mIII 0/1/1. Leg spines short, mean length of spines on tI, 0.25. Seminal receptacles (Fig. 76): bulbs paraxial, lateral slightly smaller than medial. Bulbs compact, pushed together.

Variation.—($n = 3\delta, 3\eta$) *Male*: Carapace 1.3–1.7. Little variation in CTR; rsu 4–5. Retromargin of chelicerae 7–8 teeth. *Female*: Length of carapace 1.4–1.6. Promargin of chelicerae: series of 6–7 teeth. Leg setation: fl may be 1/1/3; tl 3/1/3; fIII can have 1 dorsal macrosetae.

Natural history.—*Tetragnatha obscura* has been found only in the wet forest at low elevations on Hawaii island, in the Kahaualea natural area reserve, Puna, on the east slope of Mauna Loa.

Paratypes.—Hawaii Island, Kahaualea, 515 m, RGG & DJP, 2 January 1991, 2 δ , 2 η .

ACKNOWLEDGMENTS

The work reported here was supported by grants from the National Science Foundation, US Fish and Wildlife Service, and the University of Hawaii Research Council. Additional support was provided by the Bishop Museum, Haleakala National Park, the Nature Conservancy of Hawaii, the State Department of Land and Natural Resources, and the Hawaii Natural Areas Reserve System. For help with collecting I owe particular thanks to J. Burgett, H. Carson, B. Gagne, J. Giffin, J. Gillespie, A. Medeiros, C. Parrish, D. Preston, G. Roderick, and M. White. Finally, I owe a huge debt of gratitude to Lesley Pankaew, a very talented art student at the University of California at Berkeley, for her help with the drawings. The manuscript was much improved by comments from N. Scharff and one other reviewer.

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SHORT COMMUNICATION

A NEW SPECIES OF *PSEUDOTROGULUS* ROEWER AND ASSIGNMENT OF THE GENUS TO THE HERNANDARIINAE (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. *Pseudotrogulus funebris*, new species, is described from Estação Biológica de Paranapiacaba (Santo André, State of São Paulo, Brazil). *P. funebris* differs from other species of the genus by the presence of a large number of tubercles on area I close to the median groove, area III with tubercles concentrated in the median region, tergite III with a large rhomboid tubercle and tarsus III-IV with 8 articles. *Pseudotrogulus* is newly transferred to Hernandariinae based on the following characteristics: 1) median-anterior tubercles on anterior margin pointing upwards; 2) large tubercles on lateral-anterior margin; 3) eye mound with two tubercles upward.

Keywords: Hernandariinae, Neotropics, Opiliones, *Pseudotrogulus*.

The harvestman genus *Pseudotrogulus* Roewer (1932) was originally described in the subfamily Cranainae (Gonyleptidae). This genus remained monotypic until Kury (1992) described a second species and transferred it to the Gonyleptinae, based upon the pyriform ventral plate of the penis and the parabolic dorsal cleft. Kury (1992) discovered that the location record of the type species, *P. telluris* Roewer 1932 Caldeirão (Rio Madeira, Rondônia, Brazil) due to a mislabelling, recorded another specimen from Parque Nacional da Serra dos Órgãos (Teresópolis, Rio de Janeiro, Brazil) and described a second species, *P. mirim*, from Parati, Rio de Janeiro State, Brazil.

We here report on a new species of *Pseudotrogulus* from São Paulo, and comment on the subfamilial position of the genus. Material is lodged in Museu Nacional do Rio de Janeiro (MNRJ) and Museu de Zoologia da Universidade de São Paulo (MZSP).

Pseudotrogulus funebris new species
Figs. 1–6

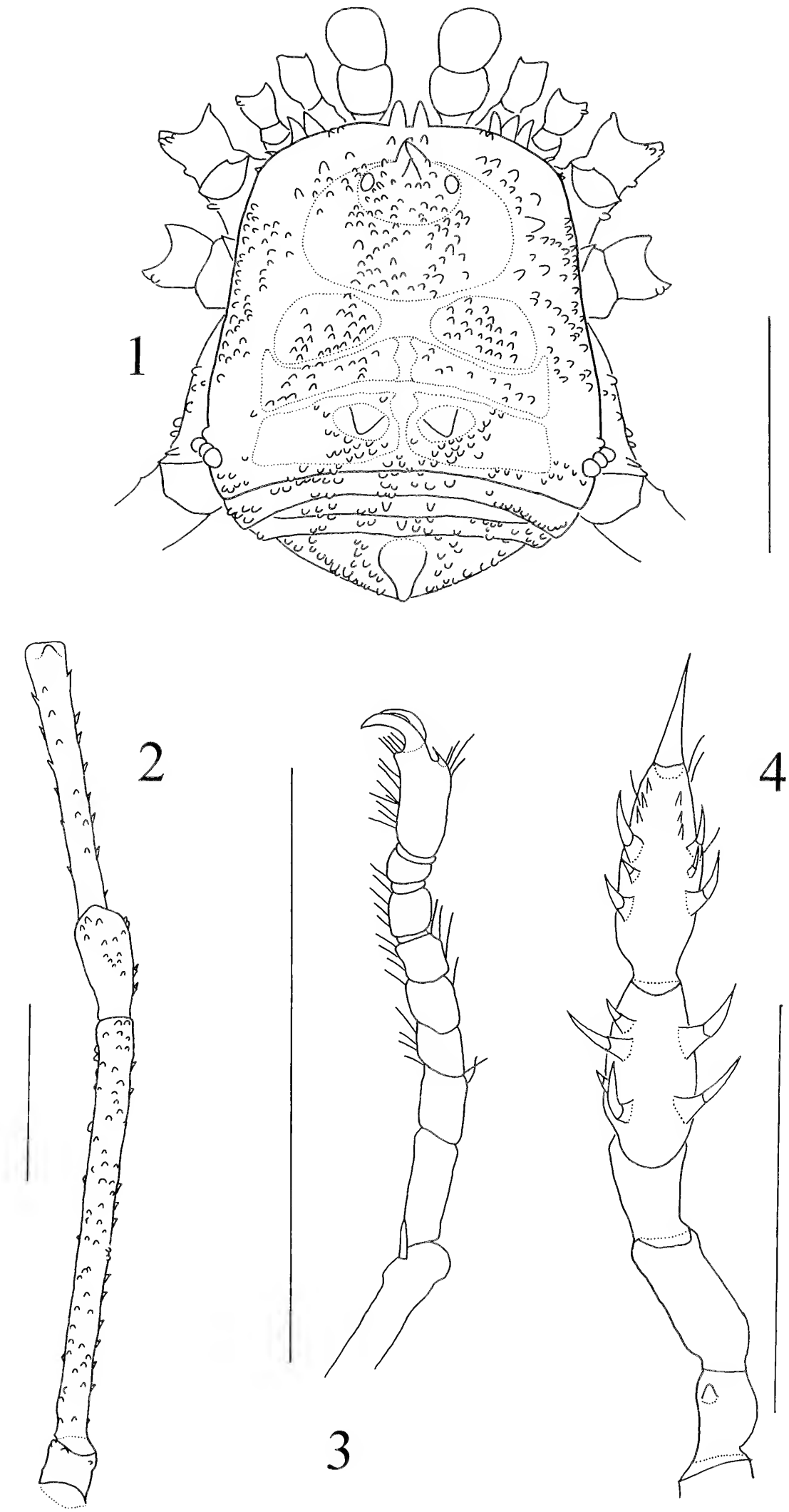
Type material.—Holotype male (MZSP 16645), 1 male paratype and 2 female paratypes (MZSP 16646) from Estação Biológica de Paranapiacaba, Santo André, São Paulo,

Brazil, 27 September 1998, R. Pinto-da-Rocha, C.L. Firmo and M.E. Chaves. 1 male paratype (MZSP 16.644), same locality, 17 May 1998, R. Pinto-da-Rocha, C.L. Firmo & R. Cordenonsi; 2 male and 2 female paratypes (MNRJ 4393), same locality, 28 December 1999, S. Reidel & R. Pinto-da-Rocha.

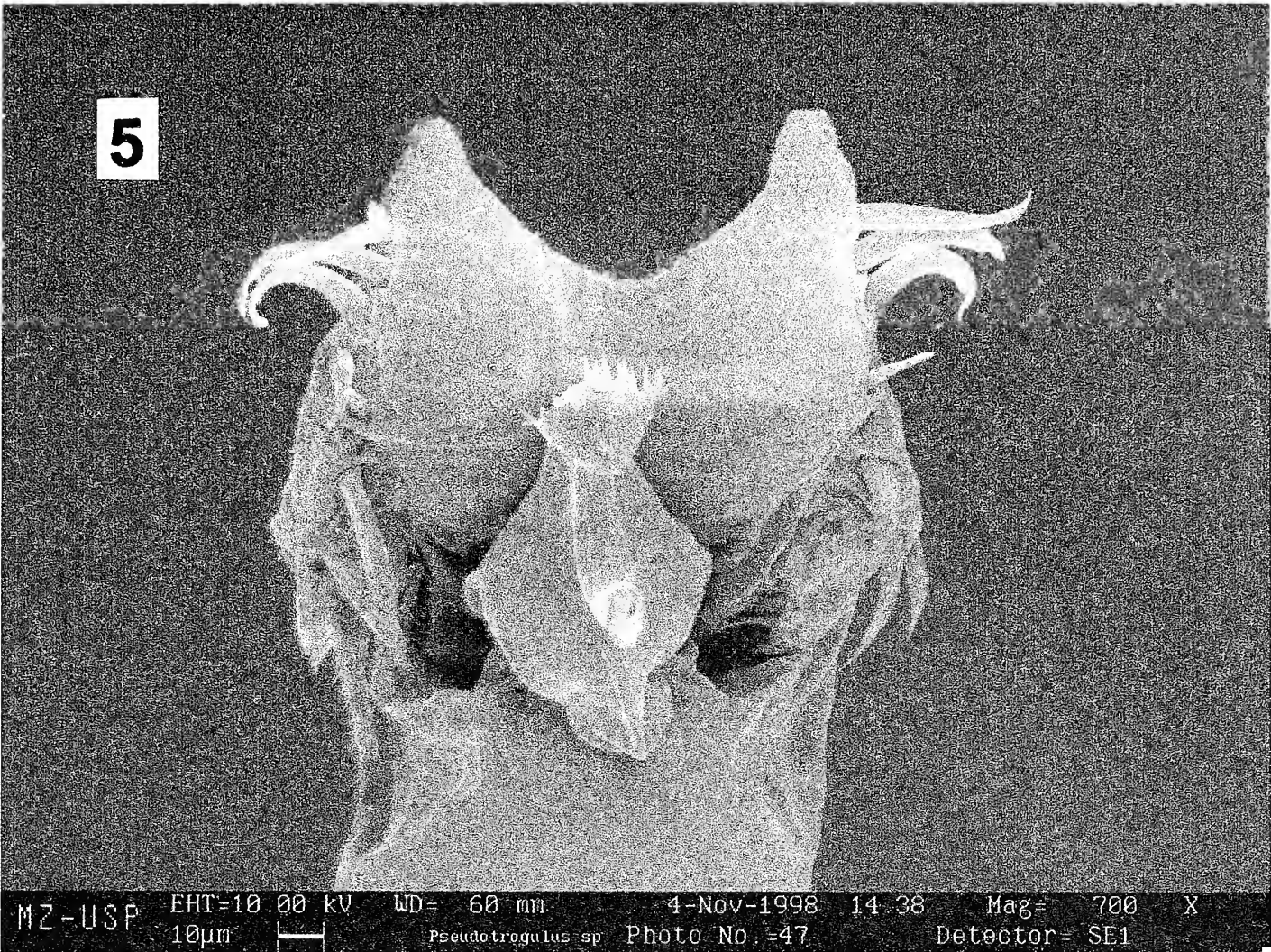
Etymology.—From the Latin *funebris*, in reference to the dark coloration and the thanatotic behavior of all species of the genus.

Diagnosis.—Differs from *P. mirim* Kury, 1992 and *P. telluris* Roewer, 1932 by the presence of a large number of tubercles on area I close to the median groove (*P. telluris* with tubercles on entire area; *P. mirim* with tubercles only close to posterior margin); area III with tubercles concentrated in the median region (tubercles in entire area in *P. telluris*, smooth in *P. mirim*); tergite III with a single large rhomboid tubercle (three large tubercles in *P. telluris* and *P. mirim*). Tarsus III-IV with 8 articles (5 in *P. telluris* and *P. mirim*).

Description.—*Male*: Measurements (in mm): Dorsal scute length 2.8; width 2.5; cephalothorax length 1.4; pedipalp 3.0; leg I 5.6; II 16.2; III 11.4; IV 15.2. *Dorsum*: (Fig. 1) Anterior margin with 2–3 tubercles on each side, central pair forward; cephalothorax with



Figures 1-4.—*Pseudotrogulus funebris* new species, male: 1. Habitus; 2. Dorsal view of trochanter-tibia IV; 3. Tarsus IV; 4. Right pedipalp. Scale bar: 2 mm.



Figures 5–6.—*Pseudotrogulus funebris* new species, penis: 5. Dorsal; 6. Lateral.

small pale tubercles, eye mound with 2 convergent spines directed; area I divided, with several tubercles on central region; area II with sparse tubercles; area III with sparse tubercles, 2 small rhomboid spines; lateral margin with tubercles from coxae III and IV, one pair larger on apex; posterior margin with tubercles sparse. Free tergite I with 26 tubercles, two central tubercles larger; II with 25 tubercles and 2 larger and a central spine; III with 1 conical spine and 36 sparse tubercles. Anal operculum with small sparse tubercles. *Venter*: Coxae I-II with 3 rows of tubercles; III-IV with sparse tubercles. *Chelicera*: Segments I-II smooth dorsally; II with sparse setae, with 7 teeth on fixed finger and 10 on movable finger. *Pedipalp*: (Fig. 4) Coxa smooth; trochanter with 1 ventral tubercle; femur smooth and slightly curved; patella smooth; tibia ectal II, mesal IiIi; tarsus ectal II, mesal IiIi. Legs (Figs. 2-3): Trochanter I with 3 tubercles; II with 8; III with 5; IV with 2. Femur I with 24 tubercles; II with 34; III with 23; IV with 62. Patellae I-II with 14 tubercles; III with 17; IV with 27 sparse tubercles (ventral and dorsal). Tibia I with 6 tubercles; II with 9; III with 10; IV with 16 tubercles. Metatarsi I-IV smooth. Tarsus I-IV 5, 9, 8, 8 segmented. *Pénis*: (Figs. 5 & 6) Ventral plate rectangular, with concave cleft on distal margin; basal lobe upwards, with 3 long and 1 short setae on each side; 4 distal setae, long and helicoidal and 1 basal short seta. Stylus cylindrical, sinuous and smooth. Ventral process diamond-shaped, distal margin serrate. *Color*: Dark brown, with dark yellow spots on entire dorsal scute, concentrated on median region of areas I-III. Chelicerae and pedipalpi bright yellow. The brown is more evident in females than in males. The legs show a variation of color from dark yellow to yellow (coxa—tarsus, respectively), less evident on females.

Female: Measurements (in mm): Dorsal scute length 3.0; width 2.8; cephalothorax length 1.4; pedipalp 3.5; leg I 6.2; II 14.5; III 11.8; IV 15.6. Female similar to male in shape of body and tubercles. Pedipalpal tibia ectal II, mesal IiIi; tarsus ectal IiI, mesal IiI. Legs uniformly dark yellow. Tarsal segmentation: 5 (3), 7 (3), 7, 7.

Remarks.—Kury (1992) transferred *Pseu-*

dotrogulus from the Cranaidae to the subfamily Gonyleptinae of the family Gonyleptidae, based upon four synapomorphies of the clade comprising Gonyleptinae, Caelopyginae, Sodreaninae, Progonyleptoidellinae and Hernandariinae. However, he did not mention any synapomorphic characters to support the subfamilial assignment. Based on an unpublished hypothesis for the subfamilies of Gonyleptidae (Pinto-da-Rocha and Kury, unpublished data), we propose here that the genus *Pseudotrogulus* is closely related to the genera *Acrogonyleptes* Roewer 1917 and *Hernandaria* Soerensen 1884 of the subfamily Hernandariinae by the following presumable synapomorphies: 1) median-anterior tubercles on anterior margin directed upwards; 2) large tubercles on lateral-anterior margin of scute; 3) eye mound with two convergent tubercles directed anteriorly; and 4) dorsal scute covered by a camouflage of dirt. The camouflage is probably held by a sticky secretion produced by the cuticle that causes sand and soil particles to adhere, similar to some Troguloida (Shear 1982). A detailed study on the subfamilial relationships will be published elsewhere by Pinto-da-Rocha and Kury (Museu Nacional do Rio de Janeiro). The preliminary analysis relates Hernandariinae to a monophyletic group formed by Progonyleptoidellinae, Sodreaninae and Caelopyginae.

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SHORT COMMUNICATION

NOTES ON THE FORAGING BEHAVIOR OF THE BRAZILIAN CAVE HARVESTMAN *GONIOSOMA SPELAEUM* (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. *Goniosoma spelaeum* (Mello-Leitão 1932) hide in caves during the day and leave periodically after dusk to forage, moving mainly vertically (towards the canopy). When stopped, individuals of all developmental stages often showed the behavior of cleaning appendages. To hunt, some specimens remained for several hours in a static posture with all legs spread out, radially disposed. In a less frequently used hunting position the body is used as a “web” i.e., the animal is supported by two opposing leaves, leaving its body between them, while legs II are kept free in the air and moving constantly. The first position possibly increasing the chance of meeting a possible prey by creating a larger area of contact, and the second especially by intercepting flying insects. Food items observed being taken in nature include: noctuid lepidopterans, tipulid and nematoceran dipterans, ascalaphid neuropterans, and isopods. They also infrequently use their chelicerae to chew on the rim of leaves and/or pieces of moss, with no ingestion of plant matter. Therefore, this behavior is probably related to drinking.

Keywords: *Goniosoma*, hunting behavior, foraging behavior, Opiliones, Gonyleptidae

The cave harvestman *Goniosoma spelaeum* (Mello-Leitão 1932) is one of the best-studied la-neatorean species, in several aspects: reproductive behavior and development (Gnaspini 1995), population ecology (Gnaspini 1996), defensive behavior (Gnaspini & Cavalheiro 1998), and morphometrics (Gnaspini 1999). Using the classification of cavernicolous animals proposed by Schinner-Racovitza (Racovitza 1907; see also Gnaspini & Hoenen 1999), *G. spelaeum* can be considered a strict troglaxene, since the individuals must leave the cave in order to forage, but must come back to the cave to breed and for shelter (Gnaspini 1996). It is restricted to caves of the Ribeira Valley in southeastern Brazil. Six nymphal stages have been recognized by Gnaspini (1995), in addition to a short larval stage and the adult stage. Its longevity was estimated to be > 40 mo.

These harvestmen hide in caves during the day and after dusk leave periodically to forage (Santos & Gnaspini, unpublished). Gnaspini (1996) recorded the food items used by *G. spelaeum* in the field (lepidopteran larvae and adults, tipulid dipterans, and ascalaphid neuropterans) and in the laboratory (banana, cooked carrot, cooked sugar beet, chopped *Tenebrio obscurus* larvae, ham, and cream cheese). On this basis the species was considered omnivo-

rous with a tendency to feed on invertebrates. However, little is known about the foraging behavior of the species, which is the aim of the present note.

We observed the nocturnal foraging behavior of *G. spelaeum* during four field trips to Barra Bonita cave, located at Parque Estadual Intervales (Ribeira River Valley, São Paulo, Brazil), carried out in different seasons (13–20 May, 06–16 July, 05–10 November, all in 1997 and 19–26 January 1998). Voucher specimens are deposited at “Museu de Zoologia da Universidade de São Paulo” (MZSP).

To allow individual recognition, all harvestmen were individually marked. We first made a round spot at the scutum using commercial ink correction fluid (Papermate “Liquid Paper Correction Pen NP10”), and then we added a number, written with a 0.1mm china ink pen (Tombow “Fineliner WS-X0-01-1”). The facts that marked animals were recaptured more than one year later and that they normally left the cave even in the same day that they were marked indicate that this marking method did not affect harvestmen survival or behavior.

The forest vegetation above the main cave entrance (up to 10 m in distance and 2 m in height) was sampled, mainly during the hours when the harvestmen leave the cave towards the epigeal environment (from 1700–2000 h), and occasionally

during their return to the cave environment (from 0300–0700 h). In addition, a given tree located close to the entrance and frequently used by the harvestmen to reach the canopy (see Gnaspini 1996) was climbed by means of a rope. Using the rope, the vegetation up to 20 m above the ground and around 6 m in diameter could also be sampled.

After leaving the cave entrance, specimens of *G. spelaeum* ($n = 97$) primarily moved vertically (towards the canopy), without a large horizontal distribution of individuals, as has also been reported for *Mitopus morio* (Fabricius 1799) (see Adams 1984). The largest horizontal distance walked was about 5 m. They walked through up to three main paths, as already noted by Gnaspini (1996), who suggested that the animals chemically mark and/or memorize their ways in and out the cave. However, we should stress that, if some kind of chemical marker is used, it seems to be individual (and not a single one used by several specimens) because different harvestmen moving towards the same given tree used different paths.

When stopped, either at their hunting places or at occasional stops while walking towards the canopy, individuals of all developmental stages often showed the behavior of cleaning appendages (“leg-threading,” see Edgar 1971). As expected, as they are considered to be essentially sensorial, the harvestmen spent the largest time cleaning legs II. Legs II were cleaned by pulling them directly between the cheliceral claws, whereas the other appendages were either cleaned directly by the chelicerae or indirectly by legs II (they first rubbed legs II on the appendage to be cleaned and afterwards cleaned legs II as mentioned before). Time spent for cleaning varied between 15–30 min in each event ($n = 11$). Cleaning behavior has also been recorded for *Leiobunum* spp., but only after the harvestmen had consumed a meal (Edgar 1971). Capocasale & Bruno-Trezza (1964) stated that harvestmen have many tactile sensorial hairs, which are more abundant on legs I and II. On the other hand, Edgar (1963) has shown that the number of sensillar organs (mainly proprioceptor organs) did not vary much among legs, at least when comparing legs II with the other legs. In any case, the cleaning behavior is probably related to the maintenance of sensorial receptors and would enhance the effectiveness of these organs to detect food and/or the sex of conspecifics (Edgar 1971).

We have confirmed the suggestion (Gnaspini 1996) that the hunting place of *G. spelaeum* is located in the tree and/or bush vegetation above the cave, mainly in the crown of the canopy, at about 20 m above the ground. No vertical stratification related to harvestmen age was observed on the vegetation, individuals of all ages have been found at different heights. In addition, the main factor influencing the beginning of hunting behavior of the

harvestmen seems not to be the height, but the fact that the animal has reached the top of the plant it climbed. On the other hand, while climbing the vegetation, these harvestmen use an exploratory behavior like that described for *Leiobunum* spp. (Edgar 1971). Therefore, during climbing they occasionally find a food item which they promptly take, suggesting an opportunistic feeding habit which includes consuming dead or dying animals.

To hunt, *G. spelaeum* adopts a static posture with all legs spread out, radially disposed. Legs I are kept straight forward, together with the pedipalps, while legs II are raised straight upwards, laterally disposed in relation to the body and perpendicular to the substrate. This position is observed in individuals of all ages ($n = 31$). It is possible that this posture increases the chance of meeting possible prey by creating a larger area of contact. Some specimens remained in this position for several hours. Others alternate stillness with some displacements, after which they return to the same position.

In a less frequently used hunting position the body is used as a “web” i.e., the animal is supported by two opposing leaves, leaving its body between them, while legs II are kept free in the air and moving constantly. This position probably increases the chance to find food, especially by intercepting flying insects. We observed a harvestmen in this position intercepting a fly in flight, but the fly was able to flee.

Harvestmen have both chemo- and mechanoreceptors on the legs (Juberthie et al. 1981; Kauri 1989), but prey capture seems to depend on physical contact and the sensorial apparatus may be not sensitive enough to detect possible prey (Phillipson 1960a). The hunting behavior of *G. spelaeum* is similar to that described for *Mitopus morio*, (Phillipson 1960a, b) and considering the postures in nature it is possible that *G. spelaeum* also depends on physical contact with the prey to start capture movements. We should mention that *Leiobunum vittatum* Say 1821 also depends on physical contact to find and recognize mates and/or mating rivals (Macías-Ordoñez 1997). Furthermore, Guffey et al. (2000) found what they interpreted to be typical innervation of chemoreceptors attached to sensillae not recognized as typical chemoreceptors (sensilla chaetica without pores, as expected) on legs of *Leiobunum nigripes* (Weed 1892).

On the other hand, some additional laboratory observation suggested that *G. spelaeum* and other harvestmen can detect prey by chemoreception since they find it very quickly (*G. spelaeum* took 30–50 seconds to reach the food placed 45 cm away) without physical contact (F.B. Oliveira pers. comm.). Perhaps closed places lead to a great concentration of chemicals, facilitating faster detection of prey. It is also possible that food items used in the laboratory (such as ham, cream cheese, and liv-

er spread) may have a stronger smell than natural items, facilitating their detection.

Because the animals cited above (Phillipson 1971; Macías-Ordoñez 1997; Guffey et al. 2000) belong to the suborder Palpatores and those studied here belong to the Laniatores, we could not discard the possibility that there are sensorial differences between them. We are presently conducting studies to check for chemoreceptors in the legs and to test food detection at distance among laneatoreans.

Our observations about the diet of *G. spelaeum* are unfortunately few, allowing only a qualitative analysis. In addition to the food items noted by Gnaspini (1996), mentioned above, we observed the use of noctuid moths ($n = 4$), nematoceran dipterans ($n = 1$) and isopods ($n = 1$). We should stress that only noctuids were included in the diet during the warmer months (November and January), whereas the variety of items increased during the colder months (May and July). Dipterans and lepidopterans had been previously recorded as food items and seem to be thoroughly used both by the laneatoreans; *Pachyloidellus goliath* (Acosta et al. 1995) and *Goniosoma longipes* (Machado et al. 2000) and the palpatoreans; *M. morio* (Phillipson 1960a; Cannata 1988), *Leiobunum* spp. (Bristowe 1949; Edgar 1971), *Oligolophus tridens* (C. L. Koch 1836) *Oligolophus agrestis* (Meade 1855) and *Phalangium opilio* (Linnaeus 1758) (Bristowe 1949). The use of isopods had been recorded only for the palpatoreans *Lacinius ephippiatus* (C. L. Koch 1835), *Leiobunum rotundum* (Latreille 1798), *M. morio*, and *Nemastoma bimaculatum* (Fabricius 1775) (Adams 1984). Finally, the use of earthworms as food items was observed in the laneatoreans *Acanthopachylus aculeatus* (Capocassale & Bruno-Trezza 1964), *Pachyloidellus goliath* (Acosta et al. 1995) and *Goniosoma longipes* (Machado et al. 2000), but was not observed for *G. spelaeum*.

Halaj & Cady (2000) suggested that it is unlikely that palpatorean harvestmen can overcome prey items much larger than themselves. If this also occurs with the apparently armed laneatoreans, larger food items, such as the lepidopterans (which are the main part of the diet of *G. spelaeum*) are probably captured still, dead or dying, while the harvestmen walk upwards to the canopy. However, a *Goniosoma* harvestmen taking prey from a spider has been recorded in the literature (Sabino & Gnaspini 1999). Hence, these harvestmen may be stronger than generally believed. Unfortunately, no case of taking large food items could be observed directly.

After taking a food item, *G. spelaeum* handles it with pedipalps and chelicerae. The handling of large prey with legs I, as noted for *Leiobunum* spp. (Edgar 1971), was not observed. Previous studies have led Gnaspini (1996) to state that individuals of *G. spelaeum* never take food items into their cave shelters. However, we observed some animals with

prey inside the cave regardless of the prey body size.

We also observed that *G. spelaeum* use their chelicerae to chew on the rim of leaves and/or pieces of moss, while walking upwards to the canopy. This was seen infrequently, and no ingestion of plant matter was observed. Therefore, we believe that the harvestmen were trying to obtain water (and other fluids) from the plants as observed for *Pachyloidellus goliath* (Acosta et al. 1995). We did not observe cannibalism among *G. spelaeum*, but we noted scavenging on conspecifics.

There seem to be large differences between the diet observed in nature and in the laboratory, as already reported for *Leiobunum* spp. (Edgar 1971), as well as the strategies used to find food. From the large number of food items both in natural and laboratory conditions, it seems that harvestmen accept a larger variety of food items in the laboratory. For instance, plant matter is commonly accepted in the laboratory, but this was never observed in nature for *G. spelaeum*, although the use of plants has been reported for some harvestmen species (see Machado & Pizo 2000). Based on the food items used in nature by *G. spelaeum*, we classify this species as a generalist carnivore with a highly opportunistic diet. However, when also considering its diet in the laboratory (see Gnaspini 1996), the species should be considered a generalist omnivore with a preference to carnivory.

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SHARING A WEB—ON THE RELATION OF SOCIALITY AND KLEPTOPARASITISM IN THERIDIID SPIDERS (THERIDIIDAE, ARANEAE)

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ABSTRACT. Sociality and kleptoparasitism occur commonly in theridiid spiders. In both behaviors a number of conspecifics occupy a single web; gregariousness entails tolerance. Sociality has evolved several times in theridiids, but kleptoparasitism seems to have arisen only once. All four or more instances of sociality in theridiids are concentrated within a clade of relatively distal theridiids. This distribution of sociality suggests common cause, i.e. the presence of some characteristics that may facilitate the evolution of social behavior. The monophyletic genus *Argyroides*, many of which are kleptoparasitic, is sister to the clade containing all social theridiids. Sociality and kleptoparasitism may thus be phylogenetically related in theridiid spiders; behaviors that facilitated the evolution of sociality could also have facilitated kleptoparasitism. Both may have their roots in maternal care.

Keywords: *Argyroides*, kleptoparasitism, maternal care, social behavior

Permanent sociality, or quasi-sociality, is known in only about 20 of the more than 37,000 described species of spiders, but based on the current classification, this represents at least 12–16 independent origins of sociality (Avilés 1997). Living in a group is atypical spider behavior; spiders are famously solitary. In most species even conspecifics are only tolerated while mating (although aggression even here is common) and as very young juveniles. Living in a group therefore requires overcoming this kind of innate aggression. Many authors have pointed out that sociality in spiders is not randomly distributed but rather concentrated in a few lineages (Shear 1970; Burgess 1978; Krafft 1979; Buskirk 1981; D’Andrea 1987; Kraus & Kraus 1988, 1990; Avilés 1997). Presumably such lineages may exhibit traits that facilitate sociality, or, in other words, predispose the spiders to group living.

Spider kleptoparasitism, the occupation of a heterospecific web to steal prey or silk, occurs in several families (Anapidae, Dictynidae, Eresidae, Sparassidae, Mysmenidae, Oonopidae, Salticidae, Symphytognathidae, Theridiidae and Uloboridae) (Struhsaker 1969; Wickler & Seibt 1988; Elgar 1993; Ramirez & Platnick 1999). Most of these instances represent opportunistic kleptoparasi-

tism by solitary spiders: the eresids *Stegodyphus africanus* (Blackwall 1866) and *S. sabulosus* Tullgren 1910 (Wickler & Seibt 1988), the salticids *Simaetha paetula* (Keyserling 1882) (Jackson 1985) and several species of *Portia* Karsch 1878 (Jackson & Blest 1982), the sparassid genus *Olios* Walckenaer 1837 (Jackson 1987) [note: Elgar (1993) presumably misread Jackson’s paper and indicates that these occur in groups], the symphytognathid *Curimagua bayano* Forster & Platnick 1977 (Vollrath 1978), the uloborid *Philoponella republicana* (Simon 1891) (Struhsaker 1969), and probably the oonopid *Oonops pulcher* Templeton 1835 (Bristowe 1958). In some cases, however, many conspecific kleptoparasites (or even a number of species of spiders and non-spider arthropods (Eberhard et al. 1993)) occupy the same host web; examples are *Sofanapis antillanca* Platnick & Forster 1989 (Anapidae) (Ramirez & Platnick 1999), *Archaeodictyna ulova* Griswold & Meikle-Griswold 1987 (Dictynidae) (Griswold & Meikle-Griswold 1987), *Isela okuncana* Griswold 1985 (Mysmenidae) and many other mysmenids (Griswold 1985; Coyle & Meigs 1989) in addition to *Argyroides* Simon 1864 (Theridiidae) (e.g. Vollrath 1987)). These animals interact frequently and

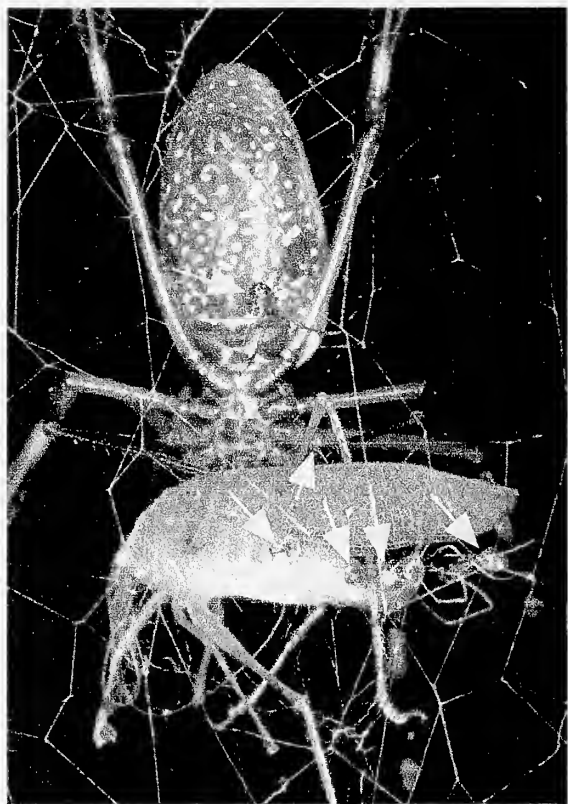


Figure 1.—Communal feeding of several individuals (arrows) of two *Argyroides* species with their host, *Nephila clavipes*.

may even feed together (Fig. 1, see also Robinson & Robinson 1973). As in sociality, such gregariousness and communal feeding must require diminished agonism.

Theridiids are behaviorally diverse, ranging from solitary web-less hunters (e.g. species of the genus *Dipoena* Thorell 1869 (Levi 1953)), to species in which thousands of individuals cooperate to build webs several cubic meters in size e.g., *Anelosimus eximius* (Keyserling 1884). Most social spider species are theridiids (Avilés 1997) as are the equally famous kleptoparasites, *Argyroides*. These are the most conspicuous spider kleptoparasites, found worldwide in the webs of *Nephila* Leach 1815, and numerous other spiders. Although both sociality and most instances of kleptoparasitism typically involve web sharing (i.e., the presence of more than one individual of the same species in a single web—excluding, of course, mating pairs) the two behaviors have hitherto been considered entirely unrelated (but see Whitehouse & Jackson 1993). Recent phylogenetic research suggests otherwise. In this paper three main points are made: first, I point out that the two types of behaviors appear phylogenetically juxtaposed in theridiid spiders; second I suggest that this may be due to a fundamental similarity between the two, namely web sharing, stemming

from maternal care; third, I discuss how the notion of web sharing implies a clear distinction between territorial and non-territorial sociality.

Although no detailed phylogeny of the family Theridiidae has ever been published, Agnarsson et al. (2001), and Arnedo et al. (2001) presented a preliminary theridiid phylogeny of 74 taxa at the XI Congress of Arachnology in Badplaas, South Africa, based on morphological and molecular data. This phylogenetic analysis will be published elsewhere, but Fig. 2 summarizes the clades relevant to this argument, based on a combined analysis of the morphological and molecular data. This arrangement has been consistently found in previous analyses. This phylogeny is included here to illustrate the argument; this admittedly speculative hypothesis does not require this particular cladistic structure to be valid.

All social theridiids occur in a relatively distal part of the cladogram, *Anelosimus* plus the “lost colulus clade” (Fig. 2). Both the current classification and the provisional phylogeny suggest at least four origins of sociality in this clade, within the genera *Theridion* Walckenaer 1805, *Achaeearanea* Strand 1929 and *Anelosimus*. The predominance of solitary *Theridion* and *Achaeearanea* species makes independent origin in these lineages very probable. Cladistic analysis further suggests a dual origin of sociality in *Anelosimus* (Fig. 2). Although not all *Argyroides* are kleptoparasites, the behavior seems to have arisen once in the common ancestor of the whole lineage (see Whitehouse et al. this volume). *Argyroides* is sister to the *Anelosimus* plus lost colulus clade. Thus all five instances of group living, or sharing a web, seem to be juxtaposed in theridiid phylogeny. Does this distribution require explanation, or is it simply coincidental? The definitive answer to this question must await the finished phylogenetic product. Maddison (1990) proposed a “concentrated changes test” to calculate the probability of obtaining, by chance alone, X independent events in a subclade of size Y in a phylogeny of Z terminals. Given the preliminary nature of both the phylogenetic and natural history data currently available, a calculation based on such data certainly cannot be definitive. However, even a marginally significant result at this point would support the notion that something unusual has occurred in this branch of theri-

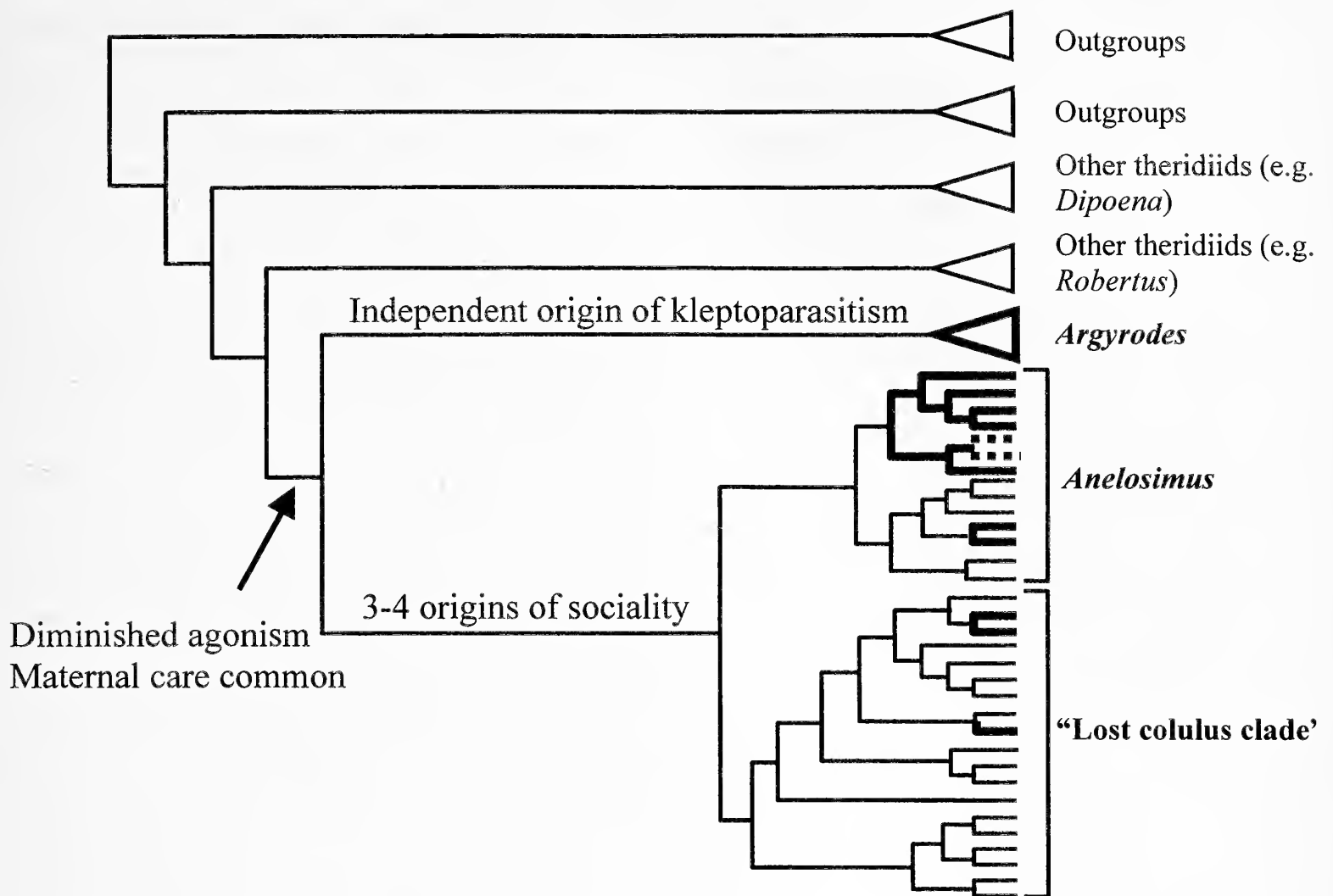


Figure 2.—Major theridiid clades ex Agnarsson et al. (2001) and Arnedo et al. (2001). Triangles represent subsidiary lineages, bold branches are group-living taxa, dotted branches unknown behavior. Web sharing (sociality plus kleptoparasitism) is notably clumped in the distal part of the cladogram suggesting a common cause.

diids, and therefore justifies some conjecture as to its genesis. In fact, the test says that sociality (four occurrences in the *Anelosimus* plus lost colulus clade) is significantly concentrated, a fact that in and by itself calls for explanation. In addition, the juxtaposition of sociality plus kleptoparasitism (five occurrences in the *Argyrodes* plus *Anelosimus* plus lost colulus clade) is significant. Of course, if the number of independent instances were to decrease in the final analysis the distribution might be attributed to chance. Likewise, augmenting the overall size of the cladogram would increase significance. As an increase in the size of the theridiid cladogram is much more certain than the discovery of novel instances of sociality or kleptoparasitism, it seems safe to conclude that their cladistic juxtaposition demands explanation if, as is argued below, sociality and kleptoparasitism are fundamentally similar. I argue that kleptoparasitism and sociality are both more likely to evolve in the presence of a trait that reduces agonism.

Many authors have argued that features required for maternal care can result in post-juvenile tolerance and sociality if siblings continue to cohabit after leaving the egg sac (Shear 1970; Kullmann 1972; Burgess 1978; Krafft 1979; Cangialosi & Uetz 1987, Avilés 1997). It should be pointed out here that maternal care is itself a vaguely defined phenomenon that may require more than one behavioral mechanism (Krafft 1982). The most obvious form of tolerance, and the one that authors presumably have in mind when they speak of the precursor to social behavior, is tolerance between peers. “Peer tolerance” among juvenile spiders is very widespread phylogenetically; most newly emerged spiderlings “tolerate” each other at least briefly (Krafft 1982). “Offspring tolerance” requires the inhibition of predation on smaller individuals, or at least on the egg sac. Finally, small spiders quite generally flee their webs if threatened by a large animal. Maternal care may additionally require inhibition of the

flight response, or “maternal tolerance” on the part of the juveniles.

Kraus & Kraus (1990) suggested that neotenic retention of juvenile tolerance “obviously” explained sociality in the eresid genus *Stegodyphus*. For example, they explained the smaller size of social *Stegodyphus* species in comparison to their solitary congeners as neoteny. In a similar manner Whitehouse (1986) suggested that kleptoparasitism might have arisen through neoteny as an extension of a fundamental “feeding with host” response of juveniles. Elgar (1993) showed that obligatory kleptoparasitic (and thus group living) *Argyroides* are smaller than their free living/opportunistic kleptoparasitic congeners, but did not claim neoteny. Both Kraus & Kraus (1990) and Elgar (1993) treated taxa as statistically independent units, which of course inflates sample size and the potential for Type I errors, due to the failure to account for shared history (Ridley 1983; Felsenstein 1985). Thus the trends on which they based their conclusions should be re-analyzed.

In this view, sociality is homologous to the juvenile tolerance exhibited in cases of maternal care. Offspring tolerance (minimally as egg sac guarding), maternal tolerance and peer tolerance seem all necessary prerequisites for maternal care but the prolongation of juvenile peer tolerance may alone explain sociality, as tolerant juveniles become tolerant adults.

Could kleptoparasitism also be modified maternal care? The latter, from the juvenile’s point of view, also means living and feeding in the web of a much bigger spider (the mother) who at some point becomes a potential predator (Whitehouse 1986). If sociality is the prolongation of the tolerance required for maternal care, kleptoparasitism can be viewed as co-opting or the exaptive application of juvenile tolerance in a novel context in which the much larger host is no longer a conspecific relative but an entirely different species. As in maternal care, the kleptoparasites (both adults and juveniles) occur in groups that feed together with the host. Interestingly, *Argyroides* kleptoparasites exhibit a wide range of “tolerance” behaviors, from obligatory kleptoparasitism in which adults tolerate the juveniles and vice versa to facultative kleptoparasites that abandon their eggsacs and presumably are opportunistically cannibalistic (Larcher & Wise 1985). In addition, kleptoparasitism in

Argyroides has other characteristics of cooperative living. Many *Argyroides* moving on the host web will produce vibratory signals from numerous directions, which may confuse the host and can be considered a form of cooperation. Such effects have been identified as benefits of sociality (Allee 1931).

As Avilés (1997) pointed out, the hypothesis that sociality evolved from maternal care predicts that sociality should be concentrated in lineages already exhibiting maternal care and that maternal care should precede sociality phylogenetically. Although more phylogenetic and natural history information is required for a strong test, current evidence does suggest that sociality in theridiid spiders is indeed concentrated in a lineage where maternal care is common. Maternal care may be necessary, but it certainly is not sufficient because it occurs in many solitary spider lineages (e.g. Araneidae (Patel & Nigam 1991), Lycosidae (Eason 1964; Fujii 1979), Oxyopidae (Randall 1977; Willey & Adler 1989), Thomisidae (Castanho & Oliveira 1997; Evans 1998), and Uloboridae (Patel & Bradoo 1981) to name but a few. Avilés (1997) pointed out that all but one of the social spiders belong to the infraorder Araneomorphae, but this is not surprising as Araneomorphae comprises the vast majority of all spiders. However, she and others have also pointed out that most social spiders build webs (Shear 1970; Krafft 1979 & 1982; Buskirk 1981; D’Andrea 1987), while about half of all spider families (and the majority of spider species) do not build prey capture webs. The importance of webs may lie with the silk itself, e.g. Krafft (1982) likened spider silk to the social pheromones of insects because the vibratory information allows communication from a distance. Krafft (1979) further suggested that sociality is relatively more common in species that build three-dimensional webs than in orb weavers. Krafft, Buskirk, and D’Andrea attributed the relative absence of sociality in orb weavers to the difficulty of cooperatively building and using an orb-web (see also Cangialosi & Uetz 1987). (Note: from the perspectives of *Argyroides* kleptoparasites, *Nephila* host orbs with their extensive barrier webs are effectively three dimensional). Theridiid web architecture varies greatly; some theridiids do not even make webs. Theridiid sociality, however, occurs

only among lineages where three dimensional webs are prevalent.

But is the concurrence of maternal care and three dimensional webs sufficient to explain why members of this particular subset of theridiids are so prone to web sharing? Other spiders beside this clade of theridiids have three dimensional webs and maternal care but lack further web sharing. Either web sharing simply has not evolved in these groups despite propitious conditions, or other unknown factors are involved, for example peer tolerance. Peer tolerance typically entails suppression of both hetero- and conspecific aggression. In a shared web, vibrations caused by conspecifics and even quite unrelated spider species walking around are generally ignored (Krafft 1982), although struggling prey, of course, trigger aggressive responses. Direct touch, however, typically triggers aggression towards heterospecific spiders only. In *Agelena consociata* Denis 1965 a pheromone on the integument seems responsible for the inhibition of mutual biting (Krafft 1975). Very little is known about spider pheromones and their possible role in social communication (see Tietjen & Rovner 1982, for review). Mutual feeding leads to exchange of digestive fluids that may contain pheromones (Krafft 1969). Kullmann (1972) suggested that contact chemoreceptors in *Stegodyphus sarasinorum* might function to receive colony pheromones. Such pheromones may be laid down on webs; recently sex pheromones have been isolated from spider webs (Schulz & Toft 1993). The study of such tolerance and communication mechanisms may cast additional light on patterns of social and kleptoparasitic web-sharing, and the relationship between the two.

The ideas presented in this paper can be tested in several ways. First, the current phylogeny juxtaposes kleptoparasitism and sociality; if the phylogeny changes in such a way that the two are no longer adjacent, behavioral homology is falsified, although maternal care might still coincide with each independently. Second, if maternal care does not evolve at the node subtending kleptoparasitism and sociality in theridiids, the hypothesis of common cause is suspect. Third, the hypothesis would be strongly corroborated if an increase in the length of time juveniles spend in their natal web evolves at the kleptoparasitism-sociality node. Fourth, this hypothesis predicts that ma-

ternal care will be common and widespread within this particular clade of theridiid spiders; at present such data are lacking for most theridiid species. Finally the ideas presented here may also apply to cases of social web sharing in unrelated spider lineages and can be tested there.

The argument followed in this paper suggests that spider "sociality" that consists of sharing a web may be fundamentally different from spider "sociality" that consists of tightly aggregated individual webs. "Web sharing" means two or more conspecifics in a single web. Whether permanent or periodic, sociality and communal kleptoparasitism are web sharing, and all might have arisen from maternal care (often labeled the "maternal care route" to sociality). In contrast, territorial "sociality," the tight concentrations of interconnected webs, differs distinctly. Known mainly from orb weavers such as *Cyclosa* Menge 1866, *Cyrtophora* Simon 1864, *Nephila*, and *Metepeira* F.O.P.-Cambridge 1903 (Burgess 1978; Krafft 1982; Aviles 1997; Burgess & Witt 1976; Burgess & Uetz 1982; Cangialosi & Uetz 1987), in these cases each individual maintains its territory (i.e., its own web) and communal feeding does not occur. Although such aggregations have been described as possibly "a colonial social organization intermediate between the solitary behavior typical of most spiders and the communal behavior of the "social" spiders" (Cangialosi & Uetz 1987 p. 237), it is not likely to be intermediate between solitariness and web-sharing sociality because it never involves web sharing. Territorial sociality in the same genus may also be periodic or permanent. *Metepeira labrynthea* (Hentz 1847) aggregates facultatively around resources, (called "fortuitous aggregations" by Buskirk & Uetz 1982), but *M. spinipes* F.O.P.-Cambridge 1903 forms permanent territorial colonies. Thus territorial "sociality" rather, as suggested by Burgess (1978), represents communal living that may arise through a different evolutionary pathway, that could be termed the "web aggregations route."

To conclude, I suggest that sociality and kleptoparasitism in theridiids can both be viewed as forms of web-sharing social behavior. The origin of both may have its roots in maternal care, via the retention of juvenile peer tolerance, sharing a three dimensional

web. Web-sharing sociality and territorial sociality seem unrelated.

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MISSING LINKS BETWEEN ARGYRONETA AND CYBAEIDAE REVEALED BY FOSSIL SPIDERS

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ABSTRACT. *Argyroneta aquatica* (Clerck 1757) should be included in Cybaeidae Simon 1898. There is no justification for a monotypic family Argyronetidae; differences from other cybaeids are either specializations for aquatic life or derived with respect to other cybaeids. The features of a recently described Eocene spider, *Vectaraneus yulei* Selden 2001 are discussed, which place it together with *Argyroneta* in subfamily Argyronetinae Thorell 1870 of Cybaeidae. Fossil spiders intermediate between *Vectaraneus* and *Argyroneta* are reviewed.

Keywords: Argyronetidae, Argyronetinae, Desidae, Eocene, England, Isle of Wight

The European water spider, *Argyroneta aquatica* (Clerck 1757) is the only spider known to live for most of its life in fresh water. Most authors (e.g. Simon 1898; Platnick 1989, 1993, 1997; Bennett 1991; Grothendieck & Kraus 1994) agree that this species is close to Cybaeidae Simon 1898, but it has been placed in a monotypic family Argyronetidae by some (e.g. Roth 1967a; and references therein), thus emphasizing the unique adaptations for aquatic life which set this species well apart from its terrestrial relatives. In this paper I briefly review the morphological adaptations to aquatism in *Argyroneta* Latreille 1804; summarize the features of a recently described Eocene spider, *Vectaraneus yulei* Selden 2001, which place it in the cybaeid subfamily Argyronetinae, also recently emended by Selden (2001); and refer to other fossil spiders which are intermediate between *Vectaraneus* Selden 2001 and *Argyroneta*.

METHODS

Material studied.—*Elvina antiqua* (von Heyden 1859), holotype BMNH 58825, Natural History Museum, London, from Miocene Brown Coal of Grube Stöschen, near Linz am Rhein, Germany. *Vectaraneus yulei* Selden 2001, holotype BMBN 021960/1, Booth Museum of Natural History, Brighton, England; paratypes: IWCMS 1999.6, Isle of Wight Museum of Geology, Sandown, Isle of Wight, England; BMNH In 17151, BMNH I 8438, BMNH I 8440 and I 8452 (part and counterpart), Natural History Museum, London, Eng-

land; all from upper Eocene Bembridge Marls ('Insect Bed') of Gurnard Bay (except IWCMS 1999.6 which is from Thorness Bay), Isle of Wight, England. The following Recent material, all in the author's collection unless stated otherwise, was studied for comparative purposes. **Agelenidae:** *Agelena labyrinthica* (Clerck 1757), female, 19 July 1990, Innsbruck University, Austria, 11°20.5'E/47°15.6'N, rough ground; *Lycosoides coarctata* (Dufour 1831), female, May 1994, SW side of Soller harbor, Mallorca, garrigue; *Tegenaria silvestris* L. Koch 1872a, male, Black Ball, Dunster, Somerset, England, SS 982425, heathland near pines. **Anyphaenidae:** *Amaurobioides maritimus* O. P.-Cambridge 1883, female, Dunedin, New Zealand (coll. California Academy of Sciences); *Anyphaena accentuata* (Walckenaer 1802), female, 10 April 1996, Carnac, France (coll. D. Penney); *Hibana similis* (Banks 1929), female, 3 December 1995, El Valle, Panama (coll. D. Penney); **Cybaeidae:** *Argyroneta aquatica* Clerck 1757, female, 18 June 1981, Whixall Moss, Shropshire, England, SJ 49–36–; male, commercial slide, compressed mount (dated 1895); *Cybaeus hesper* Chamberlin & Ivie 1932, male, 30 October 1998, Redwood grove, Monte Rio, Sonoma County, California, 38°28.811'N/123°00.275'W; *Cybaeus patritus* Bishop & Crosby 1926, female, 15 July 1996, Highlands Biological Station, Macon County, North Carolina. **Dictynidae:** *Devade* Simon 1884 sp. female, 24 May 2000, bridge on Ghara-Aghatch river, Fars Province, Iran,

52°13'E/29°41'N; *Dictyna arundinacea* Linnaeus 1758; female, 23 May 1999, Manning-tree, Essex, England, TM 081326, *Phragmites* marsh; *D. calcarata* Banks 1904, females, 30 June 1996, Wheeler Creek Nature Trail, Ventura County, California, riparian woodland; *D. innocens* O. P.-Cambridge 1872, female, 10 April 1995, Odeion, Paphos, Cyprus, 32°24'E/34°47'N; *D. reticulata* Gertsch & Ivie 1936, females, 30 June 1996, Rose Valley Lake, Ventura County California, on *Artemisia*; females, 25 August 1993, 5 mi. W of Middlegate, Nevada, 118°10'W/39°15'N, on *Artemisia*; *D. uncinata* Thorell 1856, female, 22 May 1999, Newbourne, Ipswich, Suffolk, England, TM 271435; *Lathys humilis* (Blackwall 1855), female, 22 May 1999, Newbourne, Ipswich, Suffolk, England, TM 271435; *Mallos pallidus* Banks 1904, female, 30 June 1996, Rose Valley Lake, Ventura County California, on *Artemisia*; *Tricholathys* cf. *spiralis* Chamberlin & Ivie 1935, females, 30 June 1996, Rose Valley Lake, Ventura County California, under stones in dry wash.

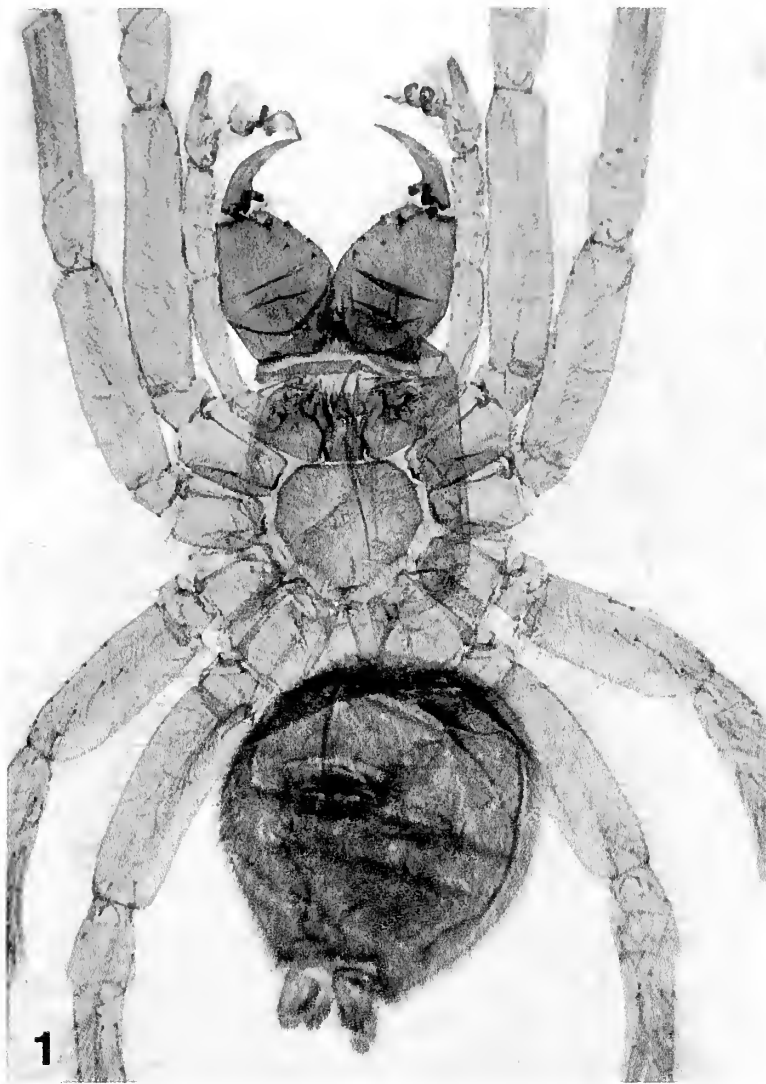
Material was studied using a Wild stereomicroscope; drawings were made with a *camera lucida* attachment; photographs were taken using a Minolta Dynax 9 camera attached to the microscope. All measurements are in mm. Abbreviations: 1, 2, 3, 4 = walking legs 1–4; AS = anterior spinneret; ch = chelicera; cx = coxa; lab = labium; MS = median spinneret; p = posterior; Pd = pedipalp; PS = posterior spinneret; st = sternum; tr = trochanter; tub = tubercle.

Argyroneta aquatica (Clerck 1757)

Remarks.—*Argyroneta aquatica* was first formally described and named by Clerck (1757:143–150; pl. 6, tab. 8, figs. 1, 2), in his genus *Araneus*, and the monotypic genus *Argyroneta* was erected for this species by Latreille (1804). Thorell (1870) created the subfamily Argyronetinae, which Menge (1871) elevated to family level in the following year. Simon (1898) recognized Argyroneteae as a tribe in Cybaeinae (Agelenidae), alongside Cybaeae and Desiae, and included the genera *Amphinecta* Simon 1898 and *Cambridgea* L. Koch 1872b in Argyroneteae. Family status for Argyronetidae was accepted by Dahl (1937), Kaston (1948), Petrunkevitch (1939) and Reimoser (1919). Kishida (1930) placed *Desis* and Cybaeinae in the family, and this

arrangement was followed by some other east Asian arachnologists, e.g. Komatsu (1961), Yaginuma (1955, 1958, 1960, 1962) and Paik & Namkung (1967). In his catalog, Bonnet (1955–9) included only the type genus, *Argyroneta*, in the family, whereas Roewer (1942–54) added *Gohia* Dalmás 1917 and *Urquhartia* Bryant 1933. Roth (1967a) both recognized and reviewed Argyronetidae, and the family status was used in the catalogs of Brignoli (1983) and Platnick (1989, 1993). However, Berland (1932), De Blauwe (1973), Gertsch (1949), Locket & Millidge (1953), Locket et al. (1974), Millot (1949) and Saito (1941) either ignored the family status or placed *Argyroneta* in Agelenidae, usually Cybaeinae (e.g. Grothendieck and Kraus 1994). Cybaeinae is commonly raised to family status in more recent works (e.g. Bennett 1991; Platnick 1993, 1997). Lehtinen (1967) limited Argyronetinae to the type genus but placed it and Cybaeinae in Dictynidae in his superfamily Amaurobioidea. Forster (1970) put Argyronetidae (also limited to *Argyroneta*) and Cybaeidae (elevated by him to family status) in Dictynoidea, but disagreed with most other authors on the close relationship between *Argyroneta* and Cybaeidae, preferring a closer alliance of *Argyroneta*, *Amaurobioidea* and Anyphaenidae. Platnick's (1997, 2001) latest catalogs put *Argyroneta* in Cybaeidae. Platnick (2001) pointed out that Argyronetidae Thorell 1870 actually has priority over Cybaeidae Banks 1892, but that the latter name is now in widespread use.

Numerous works have dealt with the aquatic mode of life and associated morphological and physiological adaptations of *A. aquatica*, especially Braun (1931, and references therein) and Crome (1953); and most works on spider respiratory physiology have studied the tracheal system of *Argyroneta*, e.g. Bertkau (1872), Bromhall (1987a), Lamy (1902) and Purcell (1910). There are a number of adaptations in *Argyroneta* for an aquatic life. A dense mat of fine setae covering the opisthosoma (Figs. 1, 2) acts as a plastron—an aquatic lung which allows air breathing under water, which works in the following way. The specialized setae (Braun 1931; Grothendieck & Kraus 1994: figs. 10–13) trap a bubble of air against the body surface and in connection with the tracheal spiracles. Oxygen diffuses from the surrounding water into the air bub-



Figures 1–2.—*Argyroneta aquatica* (Clerck 1757), adult male, microscope preparation. 1, whole body showing large chelicerae, heart-shaped sternum, long setae on base of posterior walking legs and sternum. 2, Opisthosoma showing dense felt of fine setae forming plastron, and long setae on base of posterior walking legs and sternum.

ble, which can then be exchanged in the spider's tracheal system in the normal way. Eventually, the concentrations of O_2 and CO_2 in the bubble decrease/increase respectively, so that the bubble needs to be replenished with fresh air. Long setae on the proximal podomeres of the walking legs (mainly 3 and 4) and the sternum (Figs. 1, 2) may aid in replenishing the air bubble and in carrying air to the bubble-nest. The tracheal spiracle in *Argyroneta* is rather wide and situated just posterior to the epigastric furrow. It leads to two large tracheae (Lamy 1902: fig. 56) which run forward into the prosoma before splitting into many finer tubes that extend into all parts of the prosoma, including the tarsi; similar tubules permeate the opisthosoma (Bromhall 1987a: figs. 2, 9–10), giving this spider the highest density of tracheae of any studied so far. In a study of the relationship between spider heart rates and locomotion (Bromhall 1987b), *Argyroneta* had the lowest heart rate of those studied. In general, spiders with low

heart rates have larger tracheal systems, and are either active or aquatic spiders. Presumably, gas exchange is faster when oxygen is delivered directly to tissues by the tracheal system than by intermediate transport in hemolymph. The fewer heart ostia of *Argyroneta* (Roth 1967a) might also be correlated with the diminished need for blood circulation. All of these features can be considered as adaptations for an aquatic mode of life.

Grothendieck & Kraus (1994) discussed aquatic adaptations and relationships of *Argyroneta*, and concluded that the adaptations of aquatic life were insufficient argument to separate the genus from other members of Cybaeinae (to which it is otherwise closely related, e.g. similarities in male copulatory organs), and *Argyroneta* is merely an aquatic specialized cybaeine(-id). These authors stated (Grothendieck & Kraus 1994: 272): 'Deshalb favorisieren wir die ursprüngliche Ansicht SIMONS (1898: 224, 230), wonach es sich bei *Argyroneta* um ein spezialisiertes Subtaxon

der Cybaeinae handelt. Es besteht keine Veranlassung, für die Wasserspinnne eine separate Subfamilie Argyronetinae oder gar eine Familie Argyronetidae beizubehalten. Spezielle Lebensweise und Anpassungen (insbesondere Lage des Tracheenstigmas, relativ dichte Körper-Behaarung, Zahl und Anordnung der Bothriotrichen der Laufbein-Tarsen) stellen kein Argument zur Begründung einer solchen Rangstufe dar.' [Therefore we favor the original opinion of SIMON (1898: 224, 230), according to whom *Argyroneta* occupies a specialized subtaxon of the Cybaeinae. There is no reason to maintain a separate subfamily Argyronetinae or a family Argyronetidae for the water spider. The specialized way of life and adaptations (in particular the position of the tracheal stigmata, relatively thick body setation, number and arrangement of the trichobothria of the walking-leg tarsi) do not constitute an argument in favor of such a status.]

Vectaraneus yulei Selden 2001

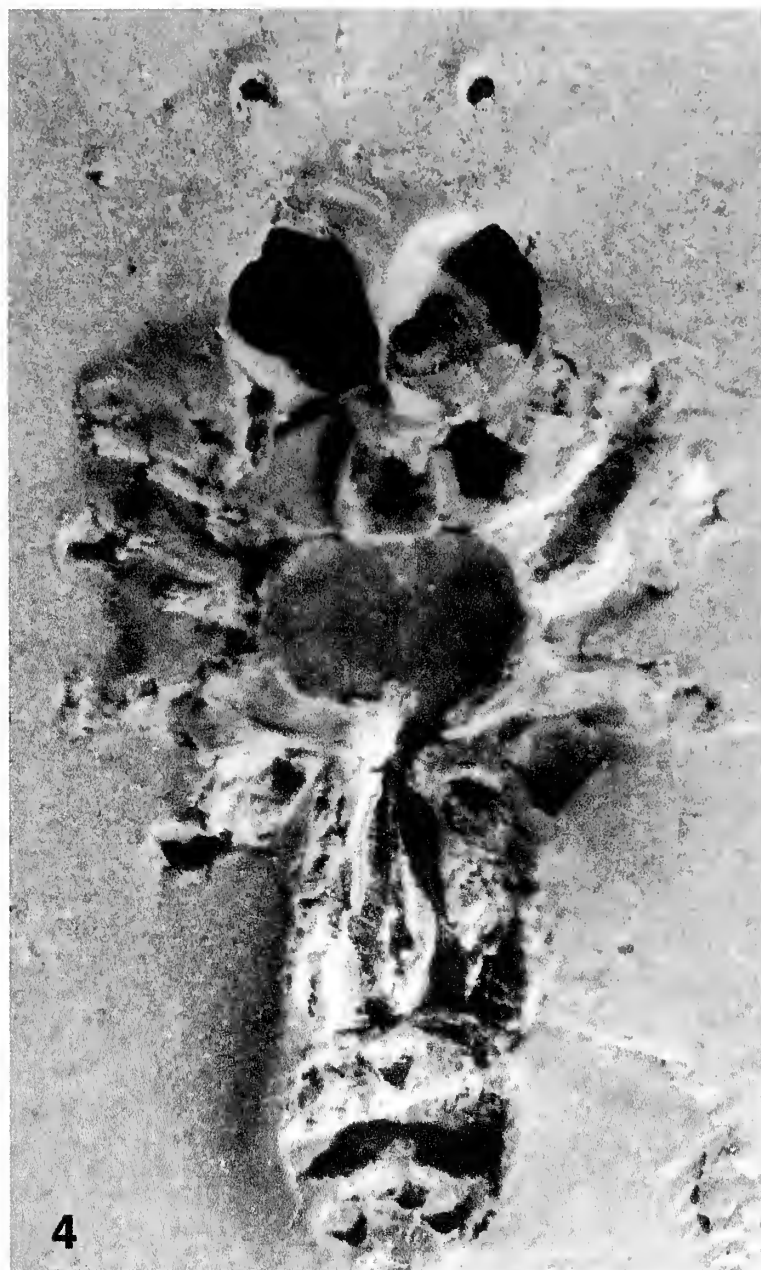
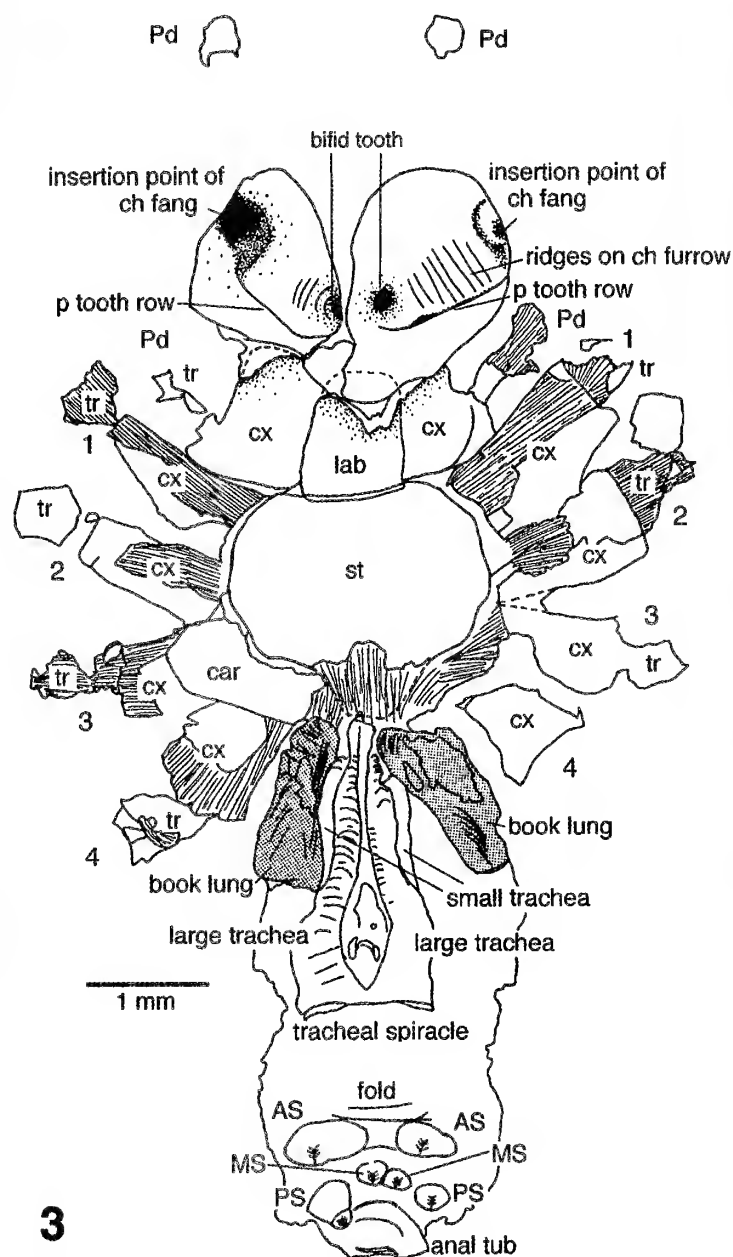
Vectaraneus yulei Selden 2001: 725–726, plates 1–5, text-figs. 1–9.

Remarks.—This taxon was erected for some fossil spiders from the so-called Insect Bed of the upper Eocene (c. 35 Ma) Bembridge Marls Member of the Bouldnor Formation (Solent Group) of Thorness Bay, Isle of Wight, England. The most remarkable aspect of the Bembridge spiders is the very fine preservation of internal anatomical structure by replacement with calcite (CaCO_3). Some organic matter is preserved, mainly cuticle lining the external mould cavities of the chelicerae and setae within the rock which can be seen when the specimens are observed under alcohol, but within the moulds of the chelicerae, labium and coxae, fine fibers of cream-colored calcite can be seen replacing muscle fibers, as described for the Bembridge Marls insects by McCobb et al. (1998). In the opisthosomae, book-lung lamellae are preserved in buff-colored calcite, and the book-lung atria anterior to the lamellae are lined with tiny, buff, drusy calcite crystals. The opisthosomae are filled with cream-colored calcite, which strikingly preserves the large tracheae running forward from a wide spiracle near the middle of the opisthosoma. The inner surfaces of these tubes bear spiral or scalariform reinforcements preserved in the same cream calcite. Spheroidal calcite filling the posterior

part of the opisthosoma of the holotype (presumably replacing silk glands or ova) was removed to reveal the spinnerets (Figs. 3, 4). Because of the preservation of internal anatomy, and their three-dimensional nature, the fossils must represent dead animals rather than molts. Detailed description of the species is given in Selden (2001) and a summary presented in Table 1, herein.

DISCUSSION

***Argyroneta* and cybaeid monophyly.**—Lehtinen (1967) was the first author to suggest the separation of Cybaeidae from Agelenidae. Following the realization that the presence of cribellum and calamistrum was plesiomorphic within Araneomorphae, he was able to place the ecribellate Cybaeinae and Argyronetinae in the cribellate Dictynidae, based on similarity of genital organs, and separate from Agelenidae. Lehtinen defined Agelenidae on a combination of three characters: paired colulus, three tarsal claws, and lengthened posterior spinnerets. Forster (1970) and Forster & Wilton (1973) carried the separation of Agelenidae from Cybaeidae further or by placing Cybaeidae and Argyronetidae in Dictynoidea but Agelenidae in Amaurobioidea, primarily on tracheal system characters. Bennett (1991) reviewed the status of Cybaeidae to that date. He suggested that secondary pores on the vulva might be a useful taxonomic character, but found that they were rather widespread in Dictynoidea (*sensu* Forster 1970), and present both in cybaeids and *Argyroneta*. He discussed the status of cybaeids in relation to Agelenidae, concluding that cybaeids shared many of the characters of agelenids: ecribellate, three tarsal claws, single row of tarsal trichobothria, unnotched trochanters, and spinnerets not in a transverse row, but that these characters were either convergent or plesiomorphic at the family level. Characters separating cybaeids from agelenids: closely spaced anterior spinnerets, and narrowed posterior spinnerets with a very short distal segment, are widespread in other spiders. As pointed out by Griswold (1990:13) "The Agelenidae has performed for three-clawed ecribellate spiders much the same function as Amaurobiidae has for cribellates: a dumping ground for obscure and undistinguished forms. Not surprisingly, identification of a synapomorphy for the Agelenidae is difficult,



Figures 3–4.—*Vectaraneus yulei* Selden 2001, holotype part, female, BMBN 021960, upper Eocene, Bembridge Marls, Isle of Wight, England. 3, Camera lucida drawing, explanation for Fig. 4; 4, Specimen after excavation of fibrous calcite replacing fine tracheae (dashed line shows rear edge of sternum); spinnerets after removal of calcite spheroids.

but I think that Lehtinen (1967:401) has proposed just such a character. He stated that all true agelenids (including the genus *Agelena*) have a paired colulus consisting of two, more or less protruding, obtusely triangular plates. I have examined many genera of Agelenidae and found this character to be a conspicuous and consistent synapomorphy.” Cybaeids and *Argyroneta* (e.g. Roth 1967a; Grothendieck & Kraus 1994) lack a colulus, but do show paired setal patches. Roth (1967b) suggested using this character in conjunction with the length of the distal segment of the posterior spinneret in the separation of agelenines and cybaeines. Bennett (1991) concluded that Cybaeidae was monophyletic on the basis of shared possession of a suite of characters not found in the same combination elsewhere, and used male palp characters to demonstrate that

the outgroup of the cybaeids probably is, or lies within, Dictynidae.

Regardless of where cybaeids are placed, and their taxonomic rank, *Argyroneta* is recognized by nearly all authorities (e.g. De Blauwe 1973; Bennett 1991; Coddington & Levi 1991; Grothendieck & Kraus 1994) to be a derived cybaeid. The position of Cybaeidae is relevant to the position of *Argyroneta* because Argyronetidae is only sustainable if Cybaeidae is monophyletic without *Argyroneta*. Bennett (1991) was unable to find an autapomorphy for all species referred to Cybaeidae, though the presence of one or more peg setae on the patellar apophysis of the male palp serves as a character which distinguishes most species. The clade defined by this character excludes *Cybaeota*, for example, which lacks a patellar apophysis but was included in

Table 1.—Comparison of features of *Vectaraneus* Selden 2001 with Anyphaenidae, Cybaeidae [*Argyroneta* in brackets], and Desidae [*Desis* in brackets]. Italics denote characters in common with *Vectaraneus*.

Feature	<i>Vectaraneus</i>	Anyphaenidae	Cybaeidae [<i>Argyroneta</i>]	Desidae [<i>Desis</i>]
Chelicera: shape	<i>vertical</i>	<i>vertical</i>	<i>vertical</i>	commonly porrect
promarginal teeth	<i>3 (1 + 1 bifid)</i>	3–6	3	<i>toothed</i>
retromarginal teeth	<i>2 + carina/denticles</i>	5–9 minute	<i>denticles [2 teeth]</i>	<i>toothed</i>
furrow	<i>broad, ribbed</i>	narrow	narrow	<i>broad</i>
condyle	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>
setal fringe	?	present	present [absent]	absent
Labium: shape	<i>longer than wide</i>	as long as wide	as long as wide	<i>longer than wide</i>
apex	<i>unnotched, rounded</i>	usually notched	<i>blunt</i>	rounded to <i>blunt</i>
basal notches	<i>present</i>	<i>present</i>	slight	<i>present</i>
Pedipalp coxa: shape	<i>rectangular</i>	<i>rectangular</i>	<i>rectangular</i>	elongate
scopula	<i>present</i>	<i>present</i>	<i>present</i>	<i>present</i> [absent]
serrula	<i>present</i>	<i>present</i>	<i>present</i>	absent
Legs: leg formula	<i>4123</i>	1423	<i>4123</i>	1423
ta claw tufts	<i>absent?</i>	lamellate	<i>absent</i>	<i>absent</i>
scopula	<i>absent</i>	dense	<i>absent</i>	weak
tr limulus	<i>unnotched</i>	notched	<i>unnotched to slightly notched</i>	notched [<i>unnotched</i>]
spines	<i>present (fe, pa, ti, mt)</i>	<i>present</i>	<i>present</i>	<i>present</i> [few on legs 1 & 2]
ta spines	<i>absent?</i>	<i>absent</i>	<i>absent</i>	present
Carapace: shape	<i>longer than wide</i>	<i>longer than wide</i>	<i>longer than wide</i>	<i>longer than wide</i>
fovea	?	longitudinal	longitudinal [weak]	distinct
Sternum: shape	<i>heart-shaped</i>	oval, apex pointed	<i>heart-shaped</i>	scutiform
precoxa triangles	<i>absent</i>	present	<i>absent</i>	<i>absent</i>
Opisthosoma: shape	<i>globular-ovoid</i>	ovoid	<i>globular</i>	ovoid
setation	<i>only normal setae</i>	plumose + normal setae	<i>normal [+ fine]</i>	fine setae only
Tracheae: extent	<i>into prosoma</i>	<i>into prosoma</i>	<i>into prosoma</i>	opisthosoma only
spiracle position	<i>median</i>	<i>median</i>	posterior [anterior]	slightly anterior to spinnerets
spiracle width	<i>broad</i>	<i>broad</i>	narrow [wide, separate]	<i>broad</i>
median trunks	<i>large, thickened</i>	<i>large</i>	normal [<i>large</i>]	normal
lateral trunks	<i>absent?</i>	present	<i>absent</i>	present
Spinnerets: position	<i>subterminal</i>	terminal	<i>subterminal</i>	terminal
AS	<i>close together</i>	contiguous	<i>close together</i>	contiguous
MS	<i>very small</i>	large	<i>very small</i>	same size as AS
PS	<i>smaller than AS</i>	cylindrical	<i>smaller than [equal to] AS</i>	equal to or longer than AS
colulus/cribellum	<i>absent</i>	group of setae	<i>absent</i>	prominent colulus/cribellum
Anal tubercle	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>	<i>distinct</i>
Total similarities with <i>Vectaraneus</i>	33	15	27 [25]	13 [12]

Cybaeidae by Bennett (1988, 1991) because it could not be placed elsewhere. *Argyroneta* has a small patellar apophysis but lacks peg setae. To summarize: Cybaeidae could be restricted to only those species which share the synapomorphy of peg setae on a patellar apophysis, which would leave at least *Cybaeota*, *Cybaeozygia* and *Argyroneta* as *incertae sedis*

within Dictynoidea, as Bennett (1991) concluded. The presently constituted Cybaeidae (e.g. Platnick 1997) encompasses these additional genera; thus the family lacks an autapomorphy but nevertheless can be defined on a suite of shared characters not found in the same combination elsewhere. Regarding *Argyroneta*, it has been pointed out by Grothendieck & Kraus (1994) that the differences between the genus and other cybaeids are almost entirely due to a secondary aquatic life. Thus, these character states are derived with respect to cybaeids, and to exclude *Argyroneta* from the Cybaeidae would render the family paraphyletic.

Looking at the differences between *Argyroneta* and *Cybaeus* in more detail [state in *Argyroneta* in brackets]. 1) setal fringe on the chelicera: present [absent]; since the setal fringe is absent in other aquatic spiders (e.g. *Desis*), it could be a hindrance in feeding and thus a derived characteristic due to aquatic life; moreover, its presence in potential outgroups (Agelenidae, Dictynidae) determines that its absence is derived. 2) a suite of characters related to the tracheal system (see Table 1), e.g. large tracheal trunks, extensive tracheation, broad spiracle, etc., are clearly related to an aquatic mode of life, and therefore derived. 3) extensive, fine setation of the abdomen (plastron) and long setae on proximal podomeres of posterior legs in *Argyroneta* are clearly derived features related to air uptake from the water surface. 4) heart ostia three pairs [two pairs] (Roth 1967a, Table 1); this reduction of heart ostia could be related to the reduced need for blood circulation because of the better tracheal penetration (cf. lower heart rate recorded for *Argyroneta* by Bromhall 1987b). 5) tarsal trichobothria in a single row [double row]; because a single row of tarsal trichobothria occurs in putative sister groups to Cybaeidae (Agelenidae and Dictynidae), a double row must be considered derived.

To conclude this discussion, Cybaeidae would be paraphyletic without *Argyroneta*; recognition of Argyronetidae with the same rank as Cybaeidae is unsustainable, but subfamily Argyronetinae could be justified. The large number of derived characters separating *Argyroneta* from other cybaeids predicts the existence of intermediate taxa.

Vectaraneus.—Of all the features of *Vectaraneus*, the wide tracheal spiracle, situated

half-way between the epigastric furrow and the base of the spinnerets, with large tracheae running forwards into the prosoma, are the most characteristic. Forster (1970) placed Amaurobioididae, Anyphaenidae, Argyronetidae, Cybaeidae, Desidae, Dictynidae, and Hahniidae in the superfamily Dictynoidea, united by their large, branched, median tracheal trunks. He pointed out that in dictynoids in which tracheal systems extend into the prosoma, spiracles occur in a more anterior position than usual; this occurs in Anyphaenidae (which includes Amaurobioididae; see Platnick 1974; Ramírez 1995), Argyronetidae, some Desidae, and Hahniidae. *Vectaraneus* is in this group of families, excluding Hahniidae because of their transverse spinnerets. Table 1 compares morphological features of *Vectaraneus*, Anyphaenidae, Cybaeidae (including *Argyroneta*), and Desidae (including *Desis*). It can be seen that *Vectaraneus* shares more character states with Cybaeidae (27/33) than with any other (see Selden 2001 for detailed discussion). It is possible that *Vectaraneus* represents another parallel development of aquatic life in a different group of spiders, but this hypothesis requires the unsubstantiated assumption of more convergence, and nearly all other characters are consistent with *Vectaraneus* being a cybaeid. As discussed above, the monophyly of Cybaeidae is not based on synapomorphies but on a unique combination of characters; *Vectaraneus* shares these characters, where they are preserved.

As discussed above, Grothendieck & Kraus (1994) considered *Argyroneta* to be a cybaeid which shows adaptations for aquatic life, including a wide, forwardly positioned, tracheal spiracle, large tracheal trunks running into prosoma and extensive tracheal system. *Vectaraneus* shows these features also, but differs in that the spiracle is situated half-way between the epigastric furrow and the spinnerets. However, the spiracle occurs in this position in juvenile *Argyroneta* (Crome 1953: figs 51–54). *Vectaraneus* also lacks the plastron. Therefore, *Vectaraneus* most closely resembles juvenile *Argyroneta*. If *Argyroneta* is a cybaeid which has become adapted to an aquatic existence, then *Vectaraneus* may be considered to occupy a part-way stage in this trend. Juvenile *Argyroneta* show a stage in the development of aquatic adaptations seen in the adult stage of *Vectaraneus*.

Other fossils referred to *Argyroneta*.—

Von Heyden (1859) described a fossil spider from the Miocene Brown Coal of Grube Stöschen, near Linz am Rheine, Germany, as *Argyroneta antiqua* von Heyden 1859, placing it in that genus on account of its general appearance and its preservation in a swampy palaeoenvironment, rather than on the basis of any characteristic morphological features, which are lacking in the fossil. Heer (1865, 1872, 1876) described a collection of spiders from the Miocene of Oeningen (Öhningen), on the border of Switzerland and Germany. A particularly long-legged form he referred to *Argyroneta*, and named *Argyronecta*? [sic.] *longipes* Heer 1865. In regard to this specimen, Heywood (footnote in Heer 1876: 11) commented: “Unfortunately the two specimens which Prof. Heer received are not sufficiently well preserved for certain determination. The comparative lengths of the legs, the thin filiform palpi, and the rounded form of the sides of the cephalothorax are in favour of it being referred to *Argyronecta* [sic.]; but the cephalothorax is less prominent in front than in the existing species. A similar form of cephalothorax and legs also occurs in *Tegenaria*. According to Thorell [1870, see below] this species does not belong in *Argyronecta* [sic.], but seems to form a distinct genus”. Thorell (1870) created the new genus *Elvina*, diagnosed by the palps being thicker than the legs, not for Heer’s specimen, but for the one described by von Heyden (1859). Thorell (1870: 224) suggested that *Argyroneta antiqua* von Heyden 1859 probably belonged in Tubitelariae (a name no longer in use for spiders which do not fall easily into any other category, including Agelenidae, Gnaphosidae, Clubionidae, Uroctidae, Filistatidae and Dysderidae), and possibly (Thorell’s emphasis) in Agelenidae: Argyronetinae. Re-study of the holotype of *Argyroneta antiqua* von Heyden 1859 by Selden (2001) concluded it is *Araeomorphae incertae sedis*, but not an *Argyroneta*, and it was referred to *Elvina* Thorell 1870. As for *A. longipes* Heer 1865, Thorell (1870) was certain that it did not belong in *Argyroneta*, and I concur.

Bertkau (1878) described a collection of fossil spiders and a millipede from the Brown Coal of Rott, including 19 specimens he referred to *Argyroneta antiqua*; ten (including von Heyden’s holotype) from the Kieselschie-



Figure 5.—*Argyroneta* sp. BMNH In 39930, Miocene Brown Coal of Rott, Germany; see Bertkau (1878).

fer (‘flint-slate’) and nine from the Blätterkohle (‘leaf-coal’). These are now distributed in a number of museums, including The Natural History Museum, London (BMNH 59627 and BMNH In 39930 (Fig. 5)), American Museum of Natural History (AMNH 26275) and the George Statz Collection in the Los Angeles County Museum of Natural History (including LACM 3086, figured by Furst 1959, 1970). Bertkau gave a detailed description of the species, including the heart-shaped sternum, and discussed the nature of prominent parallel bands (‘Längstreiffen’) on the opisthosomae of the Kieselschiefer specimens, concluding that these represented a prominent tracheal system. He suggested that the new specimens were conspecific with the holotype of *A. antiqua*, and that the species belonged in *Argyroneta* but differed from *A. aquatica* principally in that the tracheal spiracle was more posterior in position than in the type species. Bertkau was familiar with *Argyroneta*, and with spider tracheal systems in general, having published on spider respiratory organs a few years earlier (Bertkau 1872). Thus, Bertkau (1878: 359) clearly understood the importance of his conclusion that the fossils were an example of an evolutionary missing-link: “Eine Gewissheit in dieser Frage wäre allerdings von hohen Interesse, da mir der gegenwärtige Fall für die Descendenztheorie besonders lehrreich zu sein scheint.” [Certainty of this question would, however, be of great

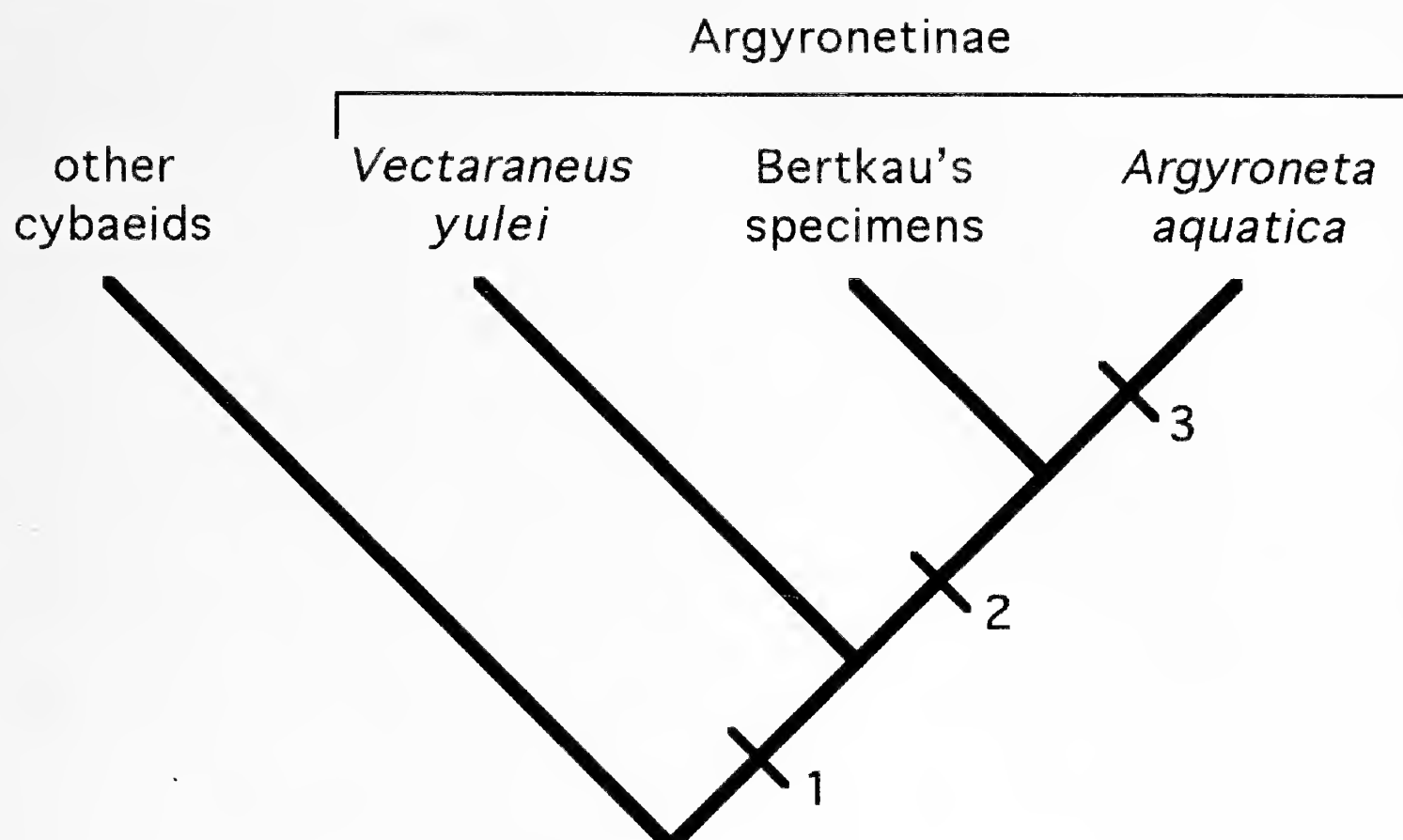


Figure 6.—Cladogram showing hypothesized relationship between *Vectaraneus yulei*, *Argyroneta aquatica*, Bertkau's specimens, and other Cybaeidae. Characters at node 1 defining Argyronetinae: enlarged tracheal trunks running into prosoma, and wide tracheal spiracle situated well forward of base of spinnerets; at node 2 (Bertkau's specimens + *A. aquatica*): dense opisthosomal pilosity (plastron), and long setae on legs 3 and 4; and at node 3 (*A. aquatica*): tracheal spiracle close to epigastric furrow in adult.

interest, since it seems to me to be a particularly instructive case of the Theory of Evolution.]

In his study of AMNH 26275, Petrunkevitch (1946) showed that this specimen was not conspecific with the holotype of *Argyroneta antiqua*, and neither are the BMNH specimens 59627 and In 39930 (Selden 2001). Bertkau's specimens are, however, close to the extant *A. aquatica*, differing, as Bertkau (1878) mentioned, by the more posterior position of the tracheal spiracle. In this, they resemble *Vectaraneus*. However, *Vectaraneus* lacks the plastron of fine hairs on the abdomen and possibly also the long hairs on the posterior two legs (the relevant podomeres are poorly preserved in *Vectaraneus*), both of which occur in the Bertkau specimens. Thus, the Bertkau specimens, which all appear to be conspecific, sit between *Vectaraneus* and modern *Argyroneta*. It is likely that they could be included in the modern genus because they share the same characters except for the more posterior position of the tracheal spiracle. No taxonomic changes are suggested here while Ph.D. research is being conducted on these specimens in Manchester by Richard Cutts. Figure 6

summarizes the phylogenetic hypothesis. Selden (2001) emended Argyronetinae as follows: "Cybaeidae with enlarged tracheal trunks running into prosoma; wide tracheal spiracle situated well forward of base of spinnerets."; included genera *Argyroneta* and *Vectaraneus*.

Mode of life.—The rock matrix preserving *Vectaraneus* is a massive, fine limestone which resembles the lithology of the main, tabular, insect-bearing horizon occurring near the base of the Bembridge Marls (Jarzembowski 1980; McCobb et al. 1998). Biota associated with the spiders include the reed *Typha*, the crustacean *Branchipodites vectensis*, Hymenoptera, Diptera, and juvenile Araneae. The arthropods are commonly in distinct horizons which suggests mass mortality, e.g. following a synchronous emergence, or aggregations accumulated by water surface tension or adhesion to floating vegetation. The palaeoenvironment of deposition suggested by the sedimentology is a shallow, freshwater, alkaline lake (McCobb et al. 1998). Associated plants, insects, and mammals suggest an open marsh habitat with wooded islands in a subtropical climate (Jarzembowski 1980; Collin-

son 1983, 1990; Collinson et al. 1993), perhaps similar to the Florida Everglades today. This evidence points to *Vectaraneus yulei* as living in a marshy habitat, and its morphological adaptations suggest it was possibly amphibious in its mode of life.

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RANGE EXPANSION OF THE HOB0 SPIDER, *TEGENARIA AGRESTIS*, IN THE NORTHWESTERN UNITED STATES (ARANEAE, AGELENIDAE)

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ABSTRACT. The hobo spider, *Tegenaria agrestis* (Walckenaer 1802), was accidentally introduced into the United States probably in Seattle, Washington during the early 1900's and gradually spread through Washington, Oregon, Idaho and into southern British Columbia during the 20th Century. Concurrent with the expansion in range, there have been reports of necrosis in humans allegedly caused by bites from *Loxosceles reclusa* Gertsch & Mulaik 1940 (which does not occur in the Pacific Northwestern U.S or Canada) or *T. agrestis*. The geographic range of *T. agrestis* now extends into Montana, Utah, Nevada and most recently, central and southwestern Wyoming.

Keywords: Hobo spider, *Tegenaria agrestis*, Agelenidae, range expansion

The hobo spider, *Tegenaria agrestis* (Walckenaer 1802), has caused considerable concern in urban areas of the Pacific Northwestern United States and southwestern Canada in recent years. In Idaho we have been inundated since the early 1990's with spider specimens from homeowners, county extension offices, schools and commercial businesses requesting identification and information. Entomologists in Utah and Washington have had similar requests (Roe 1993; Baird & Akre 1993). Coinciding with this flood of requests, there have been many reports of supposed necrotic spider bites from physicians (Vest 1987a).

Vest (1987b) reported *T. agrestis* to cause necrotic spider bite syndrome in laboratory rabbits. More recently, however, Binford (2001) stated *T. agrestis* may have been "falsely accused". Furthermore, Binford (2001) and Akre & Myhre (1991, 1994) noted that there are no authenticated cases of *T. agrestis* being positively linked to a necrotic lesion. Russell (1986), Russell & Gertsch (1983), and Vetter & Visscher (1998) showed

that the majority of diagnoses of necrosis due to spider bite are erroneous.

The medical community has often attributed these alleged spider envenomization cases to the brown recluse spider, *Loxosceles reclusa* Gertsch & Mulaik 1940, a species that does not occur and has never been collected in the northwestern United States or in Canada. Moreover, no specimens of *L. reclusa* have been collected or submitted for identification from this area. Thus, physicians who attribute bites to *L. reclusa* perpetuate misinformation causing undue fear and concern to family members and may lead to inappropriate or harmful recommendations or treatment.

METHODS

Suspected *T. agrestis* specimens were initially submitted to Vincent Roth, Portal, Arizona, Darwin Vest, Idaho Falls, Idaho, or Roger Akre, Pullman, Washington for species confirmation. Data from hundreds of *T. agrestis* specimens submitted by homeowners and county extension offices in Idaho were tabulated weekly from July through November 1992–2001 to determine seasonal activity.

We used several characters illustrated in Roth (1968) and Akre & Myhre (1991) to distinguish *T. agrestis* from *T. domestica* (Clerck 1757) and *T. duellica/saeva* Simon 1875. We relied on the male palpus and the female epi-

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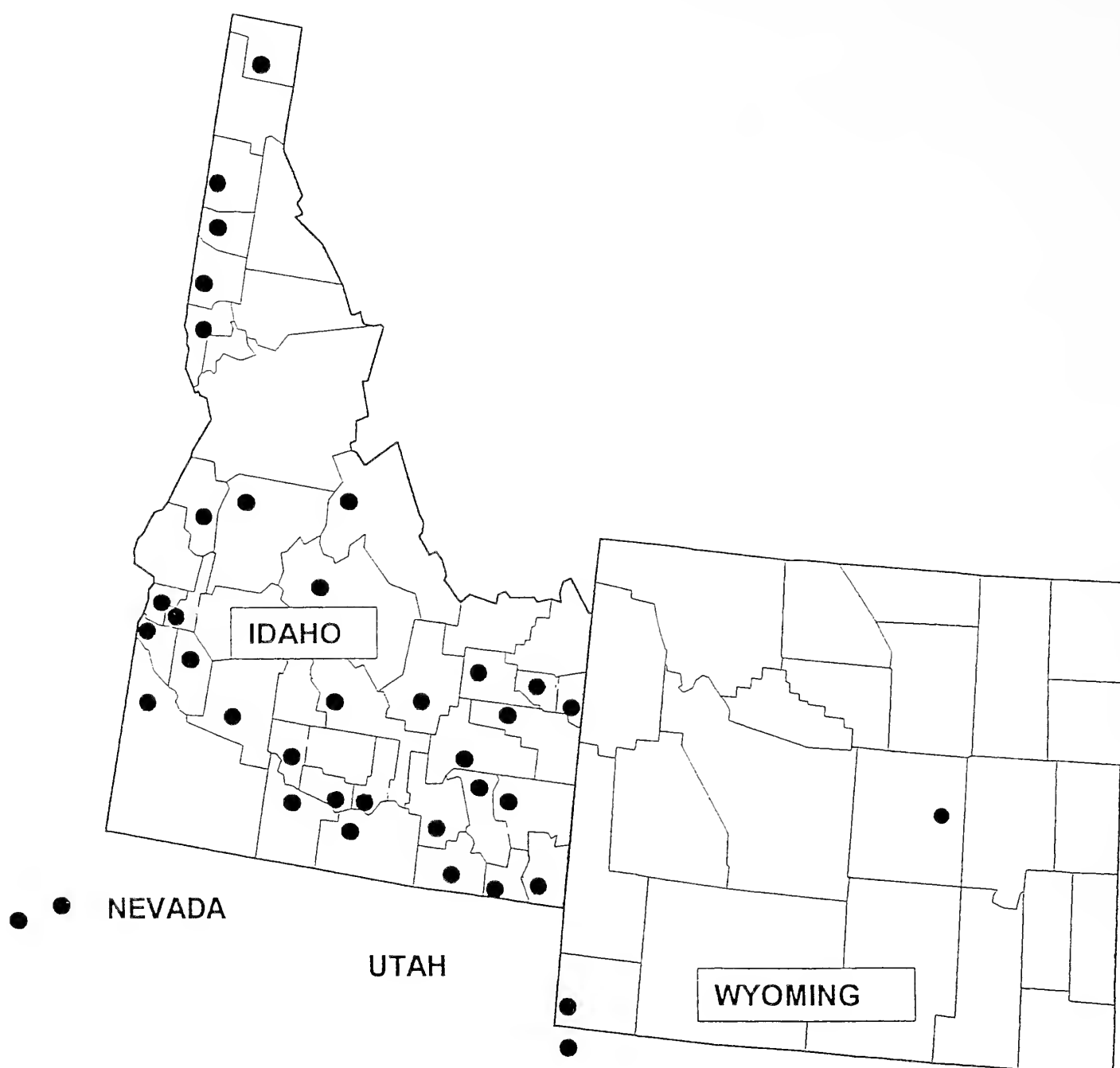


Figure 1.—Current distribution of *Tegenaria agrestis* in Idaho and Wyoming counties based on specimens submitted 1992–2001. ● = county in which *T. agrestis* has been collected. Nevada and central Wyoming locations are from singleton specimens. All other locations represent multiple collections of *T. agrestis* within that county.

gynum and the number of retromarginal teeth on the chelicerae for separation of the *Tegenaria* species. Voucher specimens are deposited in the California Academy of Sciences collection, San Francisco, California and in the W.F. Barr Entomological Collection, University of Idaho, Moscow, Idaho.

RESULTS AND DISCUSSION

Range.—*Tegenaria agrestis* has been confirmed from most Idaho counties (Fig. 1) and from most counties in Washington and Oregon (Akre et al. 1987). Bennett (pers. comm.) reports *T. agrestis* to be rare but locally abundant in various localities across extreme southern British Columbia but not yet established in Alberta. The spider has been col-

lected in the western counties of Montana extending eastward to Havre and Billings (W. Lanier pers. comm.). Vest (pers. comm.) reported *T. agrestis* in western Wyoming in 1996 predating our collection of 1 ♂ from Uinta County, southwestern Wyoming, in 1997. More recently, a single *T. agrestis* specimen (sex not documented) was confirmed in Casper (Natrona County) in central Wyoming and additional specimens (4 ♂ and 2 ♀) were submitted from southwestern Wyoming (Uinta County) in 2000 and 2001 (M. Brewer pers. comm.). The single Utah specimen (1 ♀) (Fig. 1) in our study was from Summit County where *T. agrestis* had been previously reported (Roe 1994). Utah records indicate *T. agrestis* had extended its range from the northern

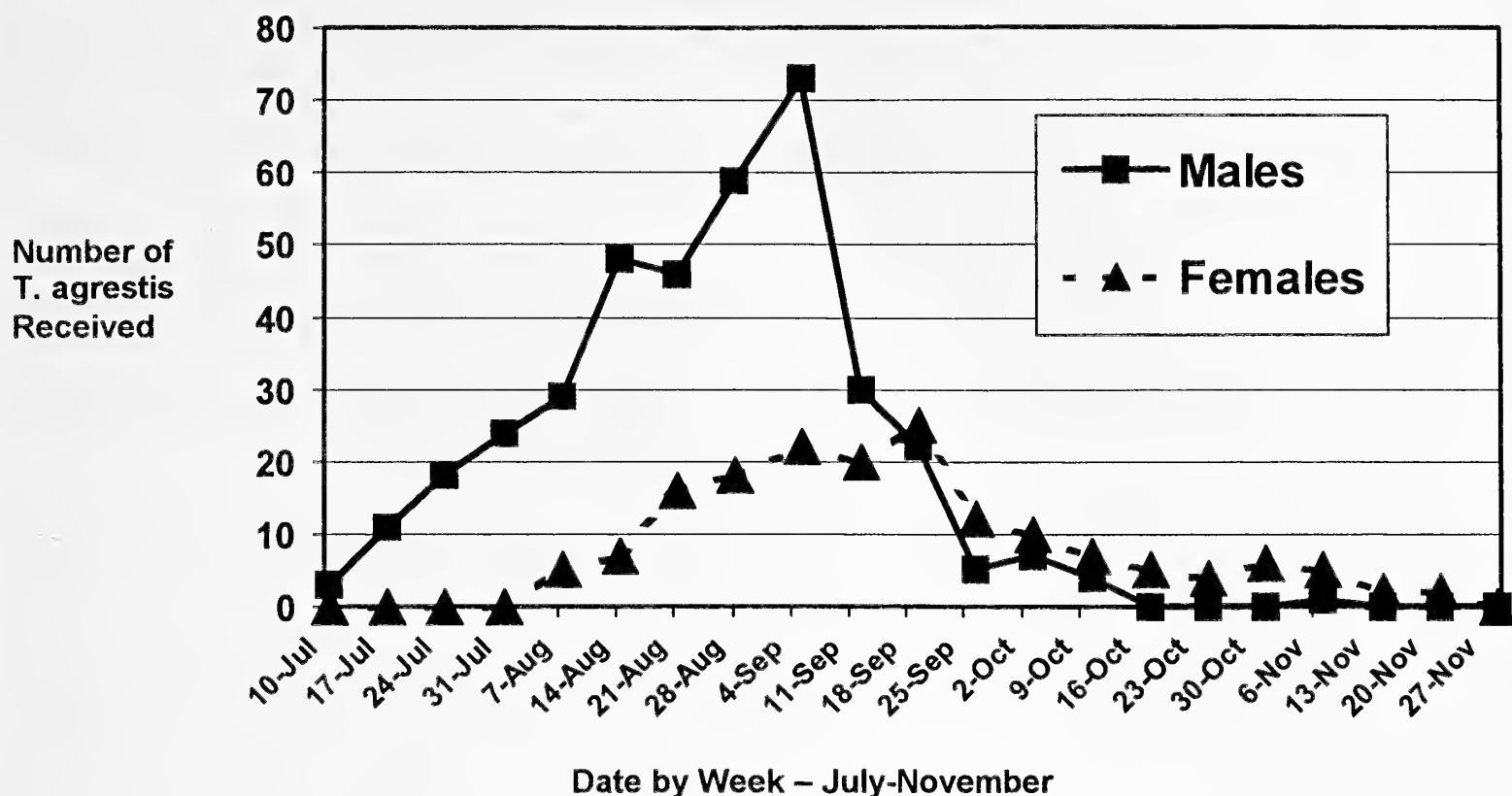


Figure 2.—Seasonal activity of *Tegenaria agrestis* adult spiders. Cumulative number of adult *T. agrestis* received weekly for identification in southern Idaho, USA, 1992–2001.

counties southward into Sanpete County by 1993. A recent collection of a *T. agrestis* specimen from San Juan County in southeastern Utah is thought to be the result of transportation of the spider in household goods and not from actual expansion of the spider's range (A. Roe pers. comm.). Single *T. agrestis* specimens were received from Winnemucca (1♂) and Lovelock (1♂), Nevada in 1995 but no other Nevada records are known. Except for the single specimens from Nevada and central Wyoming, all other locations in Fig. 1 represent multiple collections.

Season of submitted specimens.—Seasonal activity has been remarkably consistent with males being submitted beginning in early-July (Fig. 2). Corresponding with the expected normal life cycle this species, the peak of male activity was in late August and early September with declining numbers into October. Most female collections were in August and September with a peak in late September and a few specimens being submitted into November. *Tegenaria agrestis* specimens received during the fall and early winter months were fewer in number and mostly females. Of the hundreds of specimens sent to us during the 1990's, almost all were mature adults taken from human dwellings or adjacent buildings or woodpiles. Bennett (pers. comm.) reports that in British Columbia *T. agrestis* can

be very abundant in dry, open outdoor settings and may be common under driftwood above the high tide line at certain sandy beaches on southern Vancouver Island.

Observations on the diagnostic characters for distinguishing between species.—The morphology of the male palpus and female epigynum are the only truly reliable characters that will separate the North American species of *Tegenaria*. The number of teeth on the retromarginal area of the chelicerae is a dependable character for differentiating *T. domestica* and *T. agrestis*; the tooth count for *T. domestica* at three to four teeth and *T. agrestis* at five to seven teeth per retromargin. These numbers compare closely with Roth (1968) and Akre & Myhre (1991). The darker coloration and banded legs of *T. domestica* provided initial separation from lighter colored *T. agrestis* with unbanded legs in our study area. Sternal patterns as illustrated in Akre & Myhre (1991) did not allow positive identification.

Other spiders received.—Many other species of spiders were received between 1992 and 2001 in addition to the *Tegenaria* cited above. One male specimen of *T. duellica/saeva* was identified from Twin Falls County, Idaho. Other agelenids included many specimens of *Hololena nedra* Chamberlin & Ivie 1942 (det. Vincent Roth), a common house-

hold invader in southern Idaho and occasional specimens of *Agelenopsis* sp. that are common in grassy areas outdoors but seldom indoors. Other spiders submitted included theridiids *Latrodectus hesperus* (Chamberlin & Ivie 1935) and various *Steatoda* including *S. triangularis* (Walckenaer 1802) and *S. grossa* (C.L. Koch 1838) many unidentified gnaphosids and occasional clubionids including *Cheiracanthium* sp., a common inhabitant of human dwellings in southern Idaho. Many specimens of Araneidae were received including *Argiope* sp. and *Araneus* sp. and a few unidentified lycosids and salticids. Significantly absent from the hundreds of spider specimens submitted were any specimens of *Loxosceles reclusa* or other species of *Loxosceles* to which necrotic arachnidism has been erroneously attributed in the Pacific Northwest.

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DIVERSITY OF SPIDERS IN BOREAL AND ARCTIC ZONES

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ABSTRACT. During the last two decades a great number of studies dealing with arctic and boreal spiders have been published, both in the Palaearctic and the Nearctic. Such an increase in information makes it possible to analyze basic patterns of spider diversity in the North as well as to show areas where further studies are still necessary. The number of species found in faunas of larger areas north of 60°N varies from 620 (Finland) to 250 (Polar Urals) and 300 (Yukon), when island faunas are excluded. Two areas, divided by the Bering Strait, Northeastern Siberia and north-western North America have marked proportion of endemic taxa (ca. 8 %) belonging to several spider families. Considerable number of endemic spiders are known also in Middle Siberia. The number of spiders in local faunas of the boreal zone varies around 300 species. Study of species composition in more than 20 local northern faunas reveals that proportion of Lycosidae species in each local fauna varies in smallest range (7–12 % of all species found) in comparison to other families. Thus Lycosidae can be used as an indicator group of general species diversity of spiders in local faunas.

Keywords: Holarctic, diversity, indicators, northern faunas, Araneae

Spiders comprise one of the largest (5–6th) orders of animals. Spiders are also one of the best objects to study and monitor species diversity in terrestrial ecosystems, especially at high latitude (cf. Marusik & Koponen 2000). Since the early 1980's a marked number of taxonomic and faunistic reports on arctic, boreal and temperate spiders have been published both in the Palaearctic and Nearctic regions (Mikhailov 1997; Platnick 2001). This has resulted in areas that were previously almost or entirely unknown, such as the Ural mountains, Krasnoyarsk Province, Yakutia, NE Siberia, Tuva, Yukon Territory, Manitoba and British Columbia, becoming rather well-known (see Marusik et al. 2000). More than 300 spider species have been described from the Arctic and boreal zones of Asia and North America during the last 15 years. Such an increase in information makes it possible to analyze basic patterns of spider diversity in the North Holarctic, and to find the most important areas for further study. The present anal-

yses are based on literature data (Koponen 1996; Marusik & Koponen 2000; Marusik et al. 2000).

Well-studied areas and similarity.—Some well-studied faunas in different larger areas in the northern Holarctic are shown in Fig. 1. Species number varies in mainland faunas north of 60°N from 620 (Finland) to 250 (Polar Urals) and 300 (Yukon). The number of found families varies also considerable, with only 14 in the Polar Urals, 19 in the northern parts of Siberia and as high as 29 in Norway. For special features of the island faunas and their similarities, see Koponen (1993, 1995). The number of species found depends on the duration and activity of study in each area. For example, the spider fauna of Finland (620 species) has been studied more or less actively for many decades, while NE Siberia with the second largest fauna (550 species) has been investigated only for 15 years. On the basis of the known species numbers, in any larger area lying between 60° and 70°N there seem to be up to 650 spider species. Species number is higher south of the boreal zone, for example, about 900 species are

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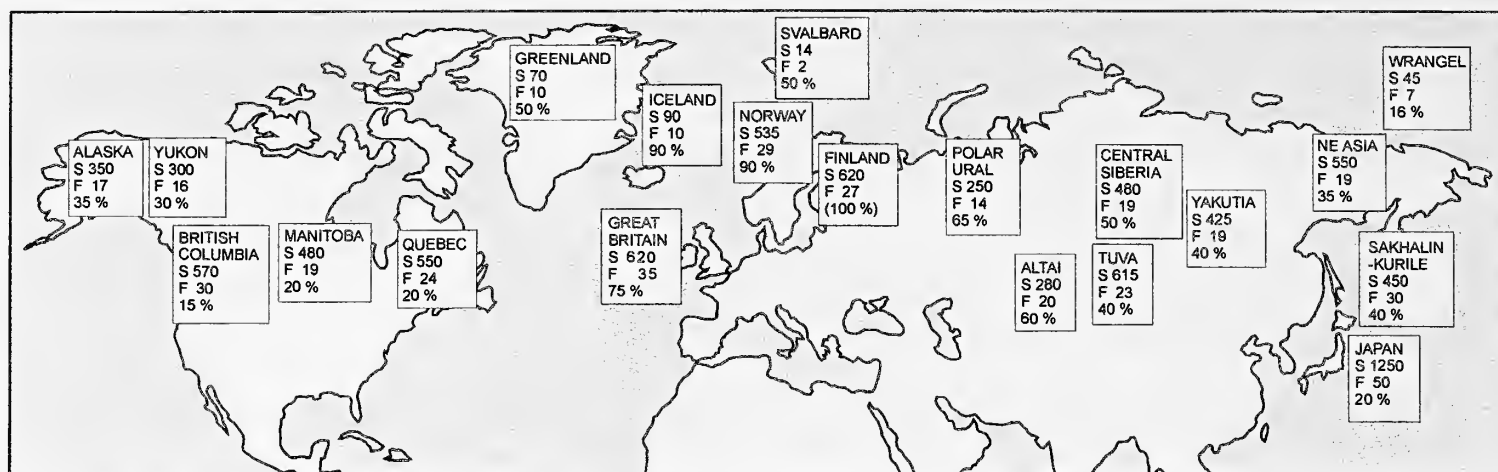


Figure 1.—Diversity of certain well-known spider faunas (S = number of species, F = number of families) and faunal similarity (as percentage of jointly occurring species) between the faunas in question and Finland (from Marusik & Koponen 2000).

known in Slovakia (Gajdos et al. 1999) and 820 in Washington (Crawford 1988 and pers. comm.).

The similarity of northern faunas is shown in Fig. 1, based mainly on data by Koponen (1996) and Marusik & Koponen (2000). The faunal similarity (as a percentage of jointly-occurring species) between Finland (a well-studied area) and select circumpolar faunas varies from 90 % in North Europe to 60 % (Altai Mts) or less in Siberia, and 15–20 % in boreal Canada. For comparison, the faunal similarity between Finland and Japan (a species and family rich area) is 20 %. The faunal similarity is correlated with the distance between sites at the same latitude; for example, 90 % similarity between Finland and Norway (ca. 700 km distance), 65 % Finland—Polar Ural (2000 km), 50 % Finland—Central Siberia (3700 km), and 40 % Finland—Yakutia (5000 km).

Faunal similarity of closely situated Beringian areas, NE Siberia and NW America is only 40 %; the proportion of jointly-occurring species varies between 36 % and 70 % in different spider families (Marusik & Koponen 2000). Extrapolating from the level of similarity between northern areas, the total worldwide number of spider species living north of 60°N latitude is about 1400–1500 species. This figure means about 4 % of the known spider species (Platnick 2001) live in an area that is 10 % of the ice-free land surface of the Earth. But about 18 % of all known linyphiids, the dominant northern spiders (Tables 1–2), live north of 60°N. When considering the faunal similarity and total species number, difficulties concerning the identity of many

problematic species in the huge circumpolar area must be borne in mind (see Koponen 1996).

Poorly studied areas.—There are still some large areas in the northern Palaearctic that could be called as unstudied “white spots” and therefore require faunistic investigations (Marusik & Koponen 2000). These include in Asia (Fig. 2): 1. West Siberia (from Ob to Yenisei), 2. Northwest Yakutia (from Kotui to Olenyok), 3. northern parts of Verkhoyanski and Cherski Mt. ranges, 4. northern part of Khabarovsk province and South Yakutia and 5. Koryakiya.

Endemism.—There are two distinct centers of endemism within the boreal zone. The highest proportion of endemic spiders is found in NE Siberia, and also in the closely situated NW North America by the Bering Strait, where about 8 % of species are endemic (Marusik & Koponen 2000). In NE Siberia more than 30 endemic linyphiid and dictynid species, restricted to the boreal zone, are known. The percentage of endemic species of staphylinid beetles in NE Siberia and NW North America is about the same (11 % and 10 % respectively; Ryabukhin 1998). The main reason for high endemism in these areas is the glaciation history of the Beringian area, it was not covered by continuous ice (e.g. Pielou 1991).

A marked number of endemic spider species is known also in Middle Siberia between Altai-Tuva (50°N) and Middle Yenisei (65°N) with about 20 endemics belonging to Linyphiidae, Lycosidae, and Gnaphosidae (Marusik et al. 2000 and Marusik, pers. obs.). In general, the percentage of endemic spiders in

Table 1.—Faunal structure of 8 local faunas in boreal zone (only species-rich families shown): 1. Tvärminne, Finland, 60°N (Palmgren 1972); 2. Nizhnesvirskiy Reserve, Russian Karelia, 60°50'N (Oliger 1996); 3. Mäntyharju, Finland, 61°15'N (Palmgren 1977); 4. Kivach Reserve, Russian Karelia, 62°18'N (Cellarius 1993); 5. Mirnoye, West Siberia, 62°20'N (Eskov 1998 and Marusik unpublished data); 6. Aborigen, East Siberia, 62°N (Marusik et al. 1992); 7. Kuusamo, Finland, 66°N (Koponen & Viramo 1998); 8. Kevo, Finland, 69°45'N (Koponen 1984); see also Fig. 2.

1. Tvär- minne	2. Ni- zhnes- virskiy		3. Mänty- harju		4. Kivatch		5. Mir- noye		6. Abori- gen		7. Kuusa- mo		8. Kevo		range of %	max./ min.		
	%	virskiy	%	harju	%	Kivatch	%	Mir- noye	%	Abori- gen	%	Kuusa- mo	%	Kevo				
Araneidae	20	5	24	7	20	6	17	6	10	4	16	4	13	5	11	6	4-7	1.75
Clubionidae	17	4	12	3	9	3	7	3	9	3	7	2	5	2	4	2	2-4	2
Dictynidae	4	1	8	2	5	2	3	1	6	2	10	3	4	2	4	2	1-3	3
Gnaphosidae	28	7	28	8	21	5	19	7	15	5	30	8	10	4	10	6	4-8	2
Hahnidae	6	1	4	1	5	2	4	1	5	2	2	1	5	2	2	1	1-2	2
Linyphiidae	176	41	141	40	145	46	129	47	156	56	198	55	135	56	98	59	40-59	1.48
Lycosidae	37	9	35	10	24	8	25	9	23	8	24	7	20	8	14	8	7-10	1.42
Philodromidae	14	3	9	3	8	3	6	2	3	1	10	3	4	2	4	2	1-3	3
Salticidae	33	8	22	6	16	5	14	5	11	4	25	7	9	4	3	2	2-8	4
Tetragnathidae	11	3	12	3	9	3	8	3	5	2	2	1	2	1	1	1	1-3	3
Theridiidae	32	8	21	6	24	6	19	7	9	3	13	4	12	5	5	3	3-8	2.7
Thomisidae	17	4	18	5	15	5	9	3	15	5	12	3	11	5	5	3	3-6	2
Total number	425		354		315		275		277		357		240		165			

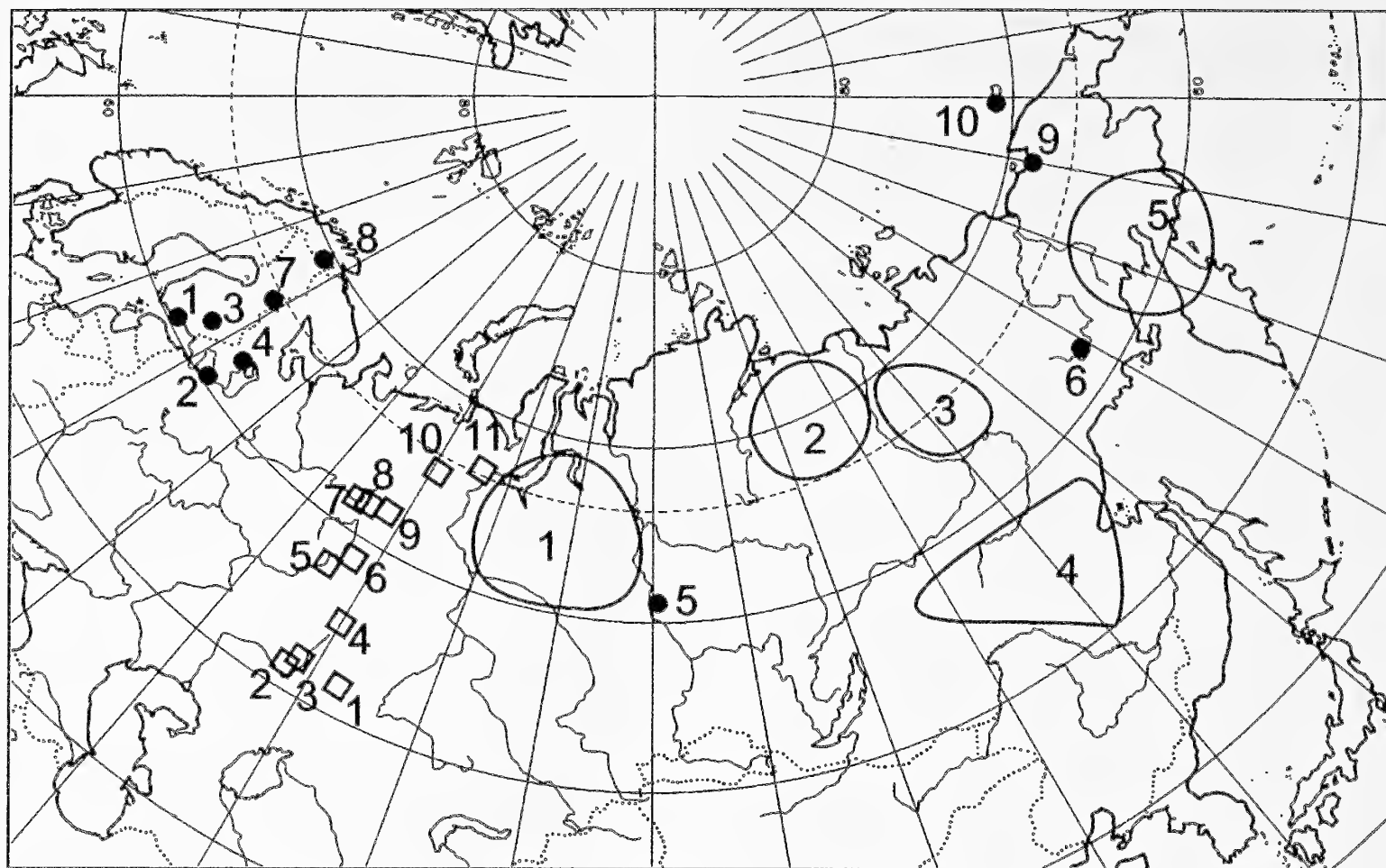


Figure 2.—Poorly known larger areas in northern Asia: 1. West Siberia; 2. Northwest Yakutia; 3. Northern Verkhoyanski and Cherski Mts; 4. North Khabarovsk and South Yakutia; 5. Koryakia. Well-studied local faunas (solid dots): 1. Tvärminne; 2. Nizhnesvirskiy; 3. Mäntyharju; 4. Kivatch; 5. Mirnoy; 6. Aborigen; 7. Kuusamo; 8. Kevo (see Table 1); 9. Chaun; 10. Wrangel. Sites in the Urals (open squares; see Table 2): 1. Troitsk; 2. Sh-Tash; 3. Bashkir Res.; 4. Ilmen Res.; 5. Preduralie Res.; 6. Basegi Res.; 7. Pechora-Lych.; 8. North Ural; 9. Lozva; 10. Cisuralia; 11. South Yamal.

larger areas of Eurasia north of 55°N does not exceed 1%.

Local faunas and indicators of diversity.—The number of species in a local fauna varies around 300 (from 240–357 species) in the boreal zone (Table 1 & Fig. 2). Tvärminne and Kevo research stations, with 425 and 165 species respectively, are at the southern and northern limits of the boreal belt in the transitional zones. Similar figures were observed in the Ural mountains (Esyunin & Efimik 1994: 240–290 species; cf. Table 2).

Some families demonstrate high fluctuation of species number and proportion within faunas compared, while the two largest families (Linyphiidae & Lycosidae) have small variation in their percentages (Tables 1–2; max./min ratio). Thus species richness of Lycosidae and Linyphiidae can be used as an indicator of the whole spider species diversity in a certain fauna. When comparing these two families in relation to absolute richness, required collecting methods and to difficulties in identification (or counting species richness) it is

clear that only wolf spiders (Lycosidae) can be used as such an indicator. Linyphiidae is the most species-rich family in each local fauna, species live in all kinds of microhabitats and therefore species survey requires different collecting methods, and also the identification of linyphiids requires experience and is time consuming. Lycosidae has more species than other families, but much fewer than Linyphiidae, and lycosids are easy to collect and identify. Species richness of wolf spiders can be rather easily revealed by using pitfall traps placed in different biotopes (habitats). The percentage of lycosids in local faunas ranges from 7–12.

When comparison of faunal structure is extended south and north of the boreal zone (e.g. to Chaun Field station in south tundra, ca. 69°N, or to Wrangel Island, arctic tundra, 71°N), only lycosids fit into criteria of good indicators of diversity (see the previous paragraph). Percentages of wolf spiders in Chaun and Wrangel are 11%, while figures for Linyphiidae are more than 70%.

Table 2. Faunal structure of 11 local faunas in the Urals (only species-rich families shown) along transection (52°30'–67°N); from Esyunin & Efimik (1994); see also Fig. 2.

	Troitsk	%	Sh.- Tash	%	Bash- kir	%	Ilmen Re- serve	%	Predur- alie	%	Basegi Res.	%	Pe- chora Lych.	%	North Ural	%	Lozva	%	Cisur- alia	%	South Yamal	%	range of max./ min	
Araneidae	23	8	19	8	19	7	18	7	22	8	14	5	21	7	18	7	11	7	2	2	3	2	2-8	4
Clubionidae	16	6	11	4	10	4	11	5	10	4	8	3	10	3	7	3	8	5	1	1	4	3	1-6	6
Dictynidae	13	5	6	2	8	3	8	3	5	2	5	2	4	1	5	2	4	3	2	2	4	3	2-5	2.5
Gnaphosidae	22	8	14	6	20	7	16	7	11	4	17	7	17	6	13	5	3	2	5	5	8	5	2-8	4
Linyphiidae	64	24	77	31	100	36	73	29	100	37	133	51	133	46	108	43	73	46	75	66	101	66	24-66	2.8
Lycosidae	28	10	24	10	28	10	22	9	22	8	23	9	33	11	30	12	12	8	13	12	17	11	8-12	1.5
Philodromidae	12	4	10	4	8	3	10	4	12	4	7	3	8	3	7	3	5	3	3	3	3	2	2-4	2
Salticidae	24	8	20	8	23	8	21	9	18	7	12	5	12	4	14	6	9	6	3	3	3	2	2-9	4.5
Theridiidae	23	8	20	8	25	9	20	8	25	9	13	5	17	6	14	6	10	6	2	2	3	2	2-8	4
Thomisidae	22	8	20	8	15	5	18	7	13	5	10	4	9	3	11	4	10	6	4	4	5	3	3-8	2.7
Total number	271		247		281		244		269		261		290		248		158		113		154			

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THE TRIGONOTARBID ARACHNID *ANTHRACOMARTUS VOELKELIANUS* (ANTHRACOMARTIDAE)

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ABSTRACT. *Anthracomartus voelkelianus* Karsch 1882 from the Pennsylvanian (Langsettian) of Nowa Ruda, Poland was listed in a 1953 monograph by Petrunkevitch as an *incertae sedis* species with type material possibly in Dresden. *Anthracomartus voelkelianus* is the type species of the genus *Anthracomartus* Karsch 1882 and historically one of the first described examples of the extinct order Trigonotarbida. It is a pivotal species for resolving the systematics of both *Anthracomartus* and a number of poorly defined, probably congeneric, taxa within Anthracomartidae. Karsch's figured types were overlooked by Petrunkevitch, but have been traced to a repository in Berlin and are redescribed here. Additional type material from Dresden and Wrocław could not be traced. One of Karsch's figured Berlin specimens is regarded here as the holotype of *A. voelkelianus*, but his other figured fossil is evidently not conspecific and is tentatively referred here to *Trigonotarbus* sp. (Trigonotarbidae).

Keywords: Trigonotarbida, Anthracomartidae, fossil, Pennsylvanian, Poland, systematics

Trigonotarbida is a group of diverse Palaeozoic arachnids recorded from late Silurian to early Permian strata, but occurring most frequently in the Coal Measures of Europe and North America. *Anthracomartus voelkelianus* Karsch 1882 was described from Pennsylvanian age rocks of Silesia (SW Poland) and is significant as the type species of *Anthracomartus* Karsch 1882, itself the type genus of Anthracomartidae Haase 1890. The systematics of this family are poorly resolved—see e.g. Dunlop & Horrocks (1996)—mostly due to Fritsch (1901, 1904) and Petrunkevitch (1945, 1949, 1953) erecting both genera and species based on what appear to be superficial and/or preservational differences. *Anthracomartus voelkelianus* is potentially the senior synonym of some of the more dubious anthracomartid species and restudy of the type material is a necessary starting point for a revision of the Anthracomartidae. There are, however, discrepancies between Karsch's (1882) two figured specimens and between Karsch's and Haase's (1890) figures of what is ostensibly the same fossil. This raises the following questions: were Karsch's original specimens conspecific, and was Fritsch's new

species, *A. granulatus* Fritsch 1904, based on some of Karsch's material? Petrunkevitch (1953) overlooked repository data in the literature, missed the opportunity to study at least some of the relevant fossils, and considered both these species to be *incertae sedis*. In this paper we aim to identify Karsch's original material and to redescribe the available type material of *A. voelkelianus*.

PREVIOUS WORK

Original descriptions.—Karsch (1882) described new fossil arachnids from the Silesian Coal Measures, above the 7th seam of the 'Rubengrube, bei Neurode, Schlesien' (= Ruben mine, near Nowa Ruda, Silesia). This locality is in southern Poland, SE of Wrocław near the border with the Czech Republic. Stratigraphically, the fossils come from the 'Schatzlarer Schichten' (= the Žacléř formation). Karsch established *Anthracomartus voelkelianus* as a new genus and species referred to a new, extinct arachnid order, Anthracomarti. Karsch named the fossils after Mr. Völkel, the pit foreman and collector of the specimens. He noted that the 'small number' of specimens were in the possession of a Mr. Schumann in Dresden, and that they were

made available to Karsch by Prof. Dames and Mr. Weiss. A repository for these fossils was not given.

Anthracomartus voelkelianus was briefly mentioned by Scudder (1884) and was subsequently redescribed and reinterpreted by Haase (1890) who, in contrast to Karsch, identified dorsal and ventral surfaces. Haase (1890, p. 645) stated (correctly) that the two specimens figured by Karsch were in the collection of the Geological Survey (formerly the Königlich-Preußische Geologische Landesanstalt) of Berlin and were lent to him (i.e., Haase) by Dames, who was director of the Geology-Palaeontology Institute of the Museum für Naturkunde (MfN) and who also worked freely for the Survey (W. Lindert, pers. comm.). Furthermore, Haase (p. 646) stated that the 'Gegendruck' (= counterpart) of Karsch's fig. 1 was in the Mineralogical Museum of Dresden, which implies that the type series was divided between at least two institutions (see also below). Haase (1890, pl. 30, fig. 9) claimed to have figured the Berlin specimen (the part) of Karsch's fig. 1, but whereas Karsch's illustration shows a fossil with a quadrate carapace and a leg, Haase's shows one with a more rounded carapace and no leg.

In his monograph of Paleozoic arachnids, Fritsch (1904) included an inverted copy of Karsch's (1882, fig. 1) illustration of *A. voelkelianus*—in Fritsch's version the leg is on the left side—and noted that the cuticle of this species is finely granulated. Note that the Czech author Anton Frič is sometimes cited under this Czech spelling of his name but, like many non-Germans in the Austro-Hungarian empire, published the papers mentioned here under the Germanized spelling 'Fritsch'. Fritsch (1904, p. 40) also created a new species, the somewhat broader *A. granulatus*, based on material in Dresden which he implied was described as *A. voelkelianus*, i.e., '... ein Exemplar das *A. Völkelianus* Fig. 2. bezeichnet war...'. Fritsch based his new species and the reconstruction (his fig. 48) on a number of specimens, but this reference to 'Fig. 2' is confusing. It could mean the fig. 2 of Karsch's plate, but this particular fossil is in Berlin (see below). It could refer to the counterpart of Karsch's fig. 2 specimen, but this specimen has been reported from Wrocław (see below). No locality for *A. granulatus* is stated, but the material is probably

also Silesian, and was described as being from 'outside Bohemia'. *Anthracomartus granulatus* was differentiated from *A. voelkelianus* on the grounds that it was shorter and wider with very clear granulation. Both species were listed in the monographs of Pocock (1911) and Petrunkevitch (1913).

In a review of the Pennsylvanian arachnids from Silesia, Schwarzbach (1935) mentioned a Westphalian age for the Rubengrube type locality. Schwarzbach noted that Karsch's type series of *A. voelkelianus* was not in Wrocław (formerly Breslau), except for the counterpart of the one figured by Karsch (1882, fig. 2). Schwarzbach cited a repository number, No. 556, for this specimen in the Geological Institute of Wrocław, which implies that Karsch's original material was divided between Berlin, Dresden and Wrocław. Schwarzbach also noted that it was uncertain whether the specimens in Karsch's two figures belonged together. Presumably he was questioning whether they were conspecific, since the literature already implied that each of Karsch's figured specimens consisted of a part and counterpart and that the specimen in Karsch's fig. 1 ended up in Berlin and Dresden (Haase 1890) while Karsch's fig. 2 ended up in Berlin and Wrocław. Schwarzbach also noted another Wrocław specimen (no. 555) as having been collected by Völkel, further supporting the idea that the original Rubengrube material ended up in more than one institution. Although originally labelled as *A. voelkelianus*, based on its wide body Schwarzbach referred no. 555 to *A. granulatus*.

Petrunkevitch's monographs.—Petrunkevitch (1949) recognized the significance of *A. voelkelianus* as the type species of *Anthracomartus*, and discussed the differences between Karsch's and Haase's interpretations (see also above). He concluded that the specimen matching Karsch's (1882, fig. 1) must be regarded as the holotype and questioned whether Karsch's two specimens were conspecific and if Karsch (fig. 1) and Haase (pl. 30, fig. 9) had actually figured the same fossil. Petrunkevitch did not study the original material, and remarked that he was unable to obtain permission to visit Dresden during a post-war tour of European museums. Correspondence in the MfN, Berlin reveals that in 1951 Petrunkevitch wrote to Alfred Kästner (then at the MfN) to ask if someone from Berlin could

visit Dresden and establish the identity of the type from the material there seen by Karsch; himself a former curator in the MfN, Berlin.

Curiously, Petrunkevitch did not ask Kästner about the Karsch types cited as being in Berlin and Wrocław. It appears that Petrunkevitch simply overlooked the repository details in Haase (1890) and Schwarzbach (1935) and assumed that all the types of both *A. voelkelianus* and *A. granulatus* were in Dresden (see also Petrunkevitch 1953), as implied by a cursory reading of both Karsch (1882) and Fritsch (1904). The unfortunate irony is that the specimens figured by Karsch were all the time in the Geological Survey of Berlin (see below), a building located at Invalidenstraße 44, adjacent to Kästner in the MfN (Invalidenstraße 43). Kästner contacted the 'Staatliches Museum für Tierkunde', Dresden, but the paleontology department there was unable to locate types of either species. Consequently, Petrunkevitch (1953, p. 68) regarded *A. voelkelianus* as an *incertae sedis* species, citing it as 'Carboniferous of Silesia. (In Dresden?)'. In fact the entire genus *Anthracomartus* became an *incertae sedis* taxon as a result of Petrunkevitch's (1953) revision, although Petrunkevitch (1955a) appeared to revalidate the taxon in the *Treatise on Invertebrate Paleontology*, listing it among the other anthracomartid genera but without any detailed discussions. An outline drawing based on Karsch's (1882, fig. 1) was included by Petrunkevitch (1955a), but since then there has been no further mention of *A. voelkelianus* in the literature.

METHODS

The Königlich-Preußische Geologische Landesanstalt is now included in the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Hannover (branch Berlin) and in 1996 the collections were moved from Invalidenstraße to a new repository at Wilhelmstraße 25–30, D-13593 Berlin. Both the type catalogues of Dienst (1928, p. 125), and more recently Daniels et al. (1998, p. 39), confirm that Karsch's material is present in this collection.

The BGR, Berlin fossils consist of the two specimens actually figured by Karsch (1882) in his original description. Both match Karsch's original illustrations, i.e. the appendages are on the correct side, and have the re-

pository numbers 09446 (Karsch's fig. 1) and 09447 (Karsch's fig. 2). The only difference is that in the original plates the specimens were drawn on larger, squarer slabs of matrix with associated plant material. The actual slabs (Figs. 1, 2) are smaller and irregular and do not look to have been trimmed, thus it appears that a certain amount of artistic licence was used in the illustrations (W. Lindert, pers. comm.). This is not to say that the drawings of the animals themselves are inaccurate (they are actually very good) only that there is a discrepancy concerning the matrix.

Specimens 09446 and 09447 are the only examples of *A. voelkelianus* in the BGR, Berlin collection. The building of the 'Geologische Landesanstalt' was damaged in the war, material was lost (W. Lindert, pers. comm.) and thus it is possible that additional specimens were originally present. Neither specimen exactly matches Haase's (1890, pl. 30, fig. 9) illustration, supposedly also of 09446, and it remains unclear what Haase actually drew. Although Petrunkevitch (1949) tended towards the idea that Haase drew a different fossil (perhaps now lost), we suspect that Haase's figure could also be based on 09446, but with the leg omitted and a different emphasis to Karsch's, more accurate, version.

Unfortunately, the material cited by Schwarzbach in Wrocław could not be traced. Martin Schwarzbach was associated with the geological institute of the University of Wrocław before the war and later material from this institute passed to the Muzeum Geologiczne (Geological Institute, Wrocław University: Cybulskiego 30, 50–205 Wrocław: A. Pacholska, pers. comm.). However, a lot of material is known to have been lost during the war, no inventory books were preserved and no fossil arachnids could be traced in the Muzeum Geologiczne collections (A. Pacholska, pers. comm.). The Wrocław material, including the possible counterpart of Karsch's figured specimen, therefore appears to be lost. Furthermore, the material cited by Haase (1890) as being in Dresden could not be traced either. In the State Museum of Mineralogy and Geology of Dresden there are several slabs with plant fossils from the Nowa Ruda site collected at the end of the 19th century. No arachnid remains could be found in them (L. Kunzmann, pers. comm.). During World War II the complete Paleozoic collec-

tion was moved to Pillnitz for safe keeping, thus loss of specimens during that time appears unlikely.

Anthracomartus voelkelianus was compared to other anthracomartid material, principally in the Natural History Museum, London (BMNH) and the National Museum Prague (NMP). The types of *A. buchi* (Goldenberg 1873) and *A. hageni* (Goldenberg 1873)—both poorly preserved, isolated trigonotarbids—were examined in the palaeontological institute of the University of Bonn (repository numbers IPB Guthörl 5 & 6), but the type of *A. granulatus* could not be found in Dresden (L. Kunzmann, pers. comm.). Specimens were drawn under alcohol using a *camera lucida*. All measurements are in mm.

GEOLOGICAL SETTING

The type material of *A. voelkelianus* comes from the Lower Silesian coal basin. This makes up a portion of the Intra-Sudetic basin, the largest geological unit in the Middle Sudetes. The Pennsylvanian sedimentary succession of the Intra-Sudetic basin is distinctly differentiated into several complexes of different clastic material composition, color and paleontological inventory (Bossowski et al. 1995). The first lithostratigraphic subdivision was proposed in the 19th century and was based on informal mining terminology. The sediments of the Žacléř formation, from which the *A. voelkelianus* fossils were obtained, were accumulated under a fluvio-lacustrine regime and represent sub-environments of river channels of low and high sinuosity. In the vicinity of Nowa Ruda the lower (Langsettian age) portion of the Žacléř formation is dominated by fine-grained clastics that contain as many as 20 coal seams. The origin of the coal-bearing sequence, whose thickness reaches 160 m, was peat swamp development in extended alluvial plains. The upper (Duckmantian age) portion of the Žacléř formation is as much as 230 m thick and is composed primarily of coarse-grained clastics. Today it is difficult to say exactly where the 7th seam of the 1882 terminology should be placed within the sequence. All indications point to the lower Žacléř formation (upper Langsettian age, [= Westphalian A]) in recent terminology.

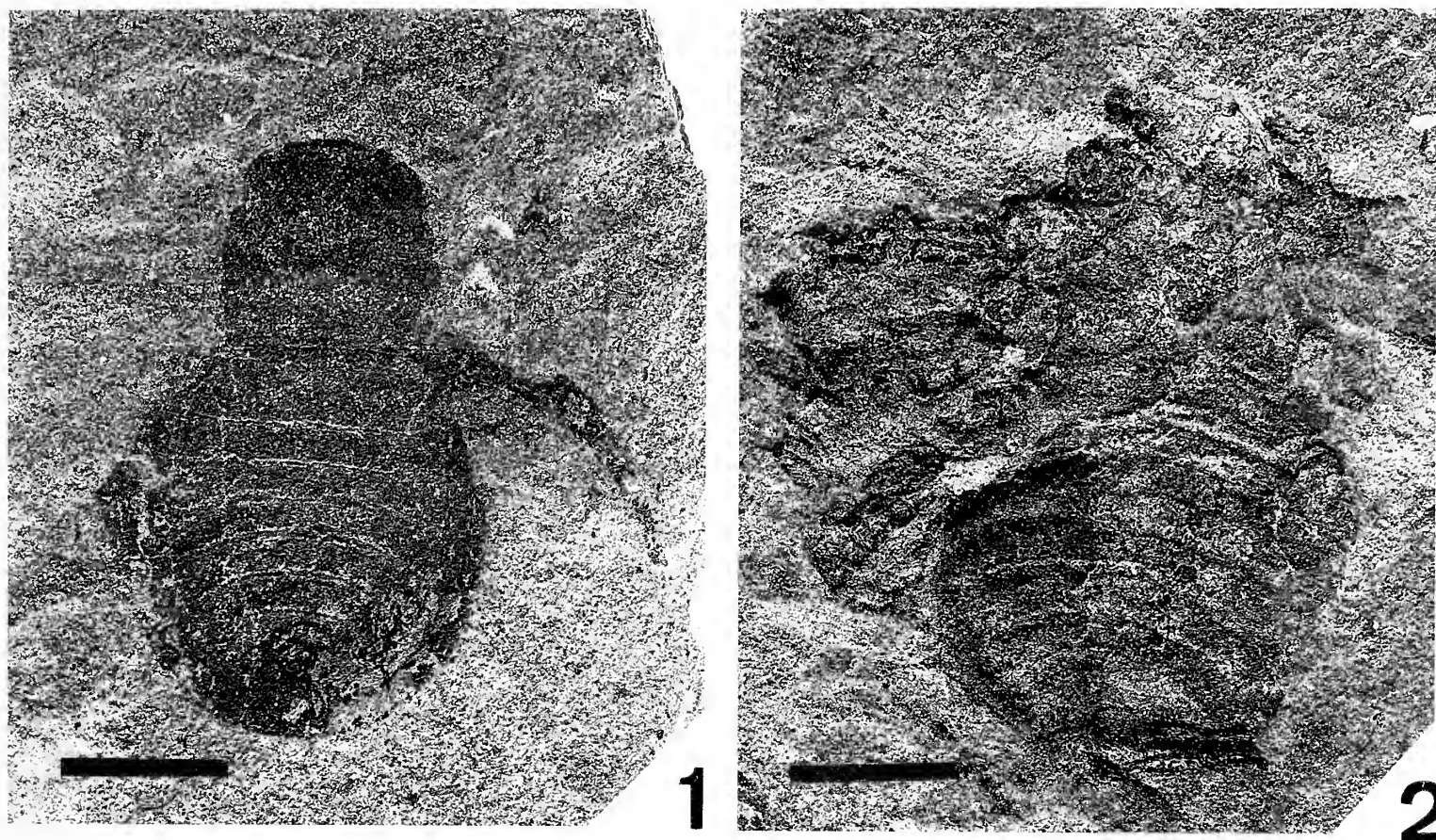
SYSTEMATIC PALEONTOLOGY

Order Trigonotarbida Petrunkevitch 1949

Remarks.—Petrunkevitch (1949) divided Anthracomarti into two orders: Anthracomartida and Trigonotarbida. The features he used to separate these taxa were rejected by Dunlop (1996) as either misinterpretations of the fossils or as insufficient grounds for maintaining distinct orders. They were reunited under the more clearly defined Trigonotarbida, with Anthracomartidae representing one family, diagnosed on tergites divided laterally into 5 plates as opposed to 3 plates in all other trigonotarbids (see Dunlop 1996 for further discussions).

Family Anthracomartidae Haase 1890

Remarks.—Following Petrunkevitch (1953, 1955a), the family Anthracomartidae includes nine valid genera. Two of these, *Brachypygus* Woodward 1878 (known only from an opisthosoma) and *Maiocercus* Pocock 1911 are both distinct in having a scalloped opisthosomal margin (see also Dunlop & Horrocks 1996). Most of the remaining genera: *Promygalus* Fritsch 1901, *Brachylycosa* Fritsch 1904, *Coryphomartus* Petrunkevitch 1913, *Pleomartus* Petrunkevitch 1945, *Cleptomartus* Petrunkevitch 1949, *Cryptomartus* Petrunkevitch 1949 and *Oomartus* Petrunkevitch 1953 were based on specimens which were either originally, or at some stage (Pocock 1910), referred to *Anthracomartus*; an *incertae sedis* taxon in Petrunkevitch's (1953) scheme. In his key in this paper, Petrunkevitch diagnosed the anthracomartid genera based mostly on carapace morphology, but provisional work suggests that many of the supposed differences between the carapaces are preservational artifacts, typically based on missing features and strongly influenced by whether the fossils were compressed to a greater or lesser extent in shales or preserved more three-dimensionally in ironstone concretions. The taxonomy of the flattened Nýřany material in Prague is especially suspect and includes specimens, probably identified by Petrunkevitch, (NMP A/165b & A/22b) where the part and counterpart have been assigned to different genera. This study revalidates *Anthracomartus*, rediagnosed below based on the redescription of the genotype. *Anthracomartus*



Figures 1–2.—Photographs of Karsch's fossils housed in the BGR, Berlin. Both from the Pennsylvanian (Langsettian) of the Ruben mine, Nowa Ruda, Intra-Sudetic basin, Poland. 1, No. 09446, holotype of *A. voelkelianus*; 2, No. 09447, a specimen which is not the counterpart of, nor even conspecific with, 09446 and which is referred here to? *Trigonotarbus* sp. Scale = 5 mm.

is potentially the senior synonym of some of these poorly diagnosed anthracomartid genera.

Anthracomartus Karsch 1882

Type species.—*Anthracomartus voelkelianus* Karsch 1882

Included species.—*Anthracomartus granulatus* Fritsch 1904, *A. buchi* (Goldenberg 1873) and *A. hageni* (Goldenberg 1873), the latter two species both *nomina dubia*.

Emended diagnosis.—Anthracomartids with a smooth opisthosomal margin, lacking the marginal scalloping seen in *Brachypyge* and *Maiocercus*. The status of the remaining anthracomartid genera (see above) is questionable and merits revision.

Remarks.—The two Goldenberg species were referred to *Anthracomartus* by Guthörl (1934), but they are based on poor specimens (IPB Guthörl 5 & 6) which are effectively unidentifiable (Petrunkévitch 1953). Both are regarded here as *nomina dubia*. To date, we have been unable to trace the type of *A. granulatus*, supposedly in Dresden (see above), thus we have been unable to confirm its generic affinities.

Anthracomartus voelkelianus Karsch 1882

Figs. 1, 3

Anthracomartus Völkelianus Karsch 1882: 560–561, pl. 21, fig. 1; Scudder 1884:14, 17; Haase 1890: 645–646. Pl. 30, figs. 8, 9; Fritsch 1904: 40, fig. 47.

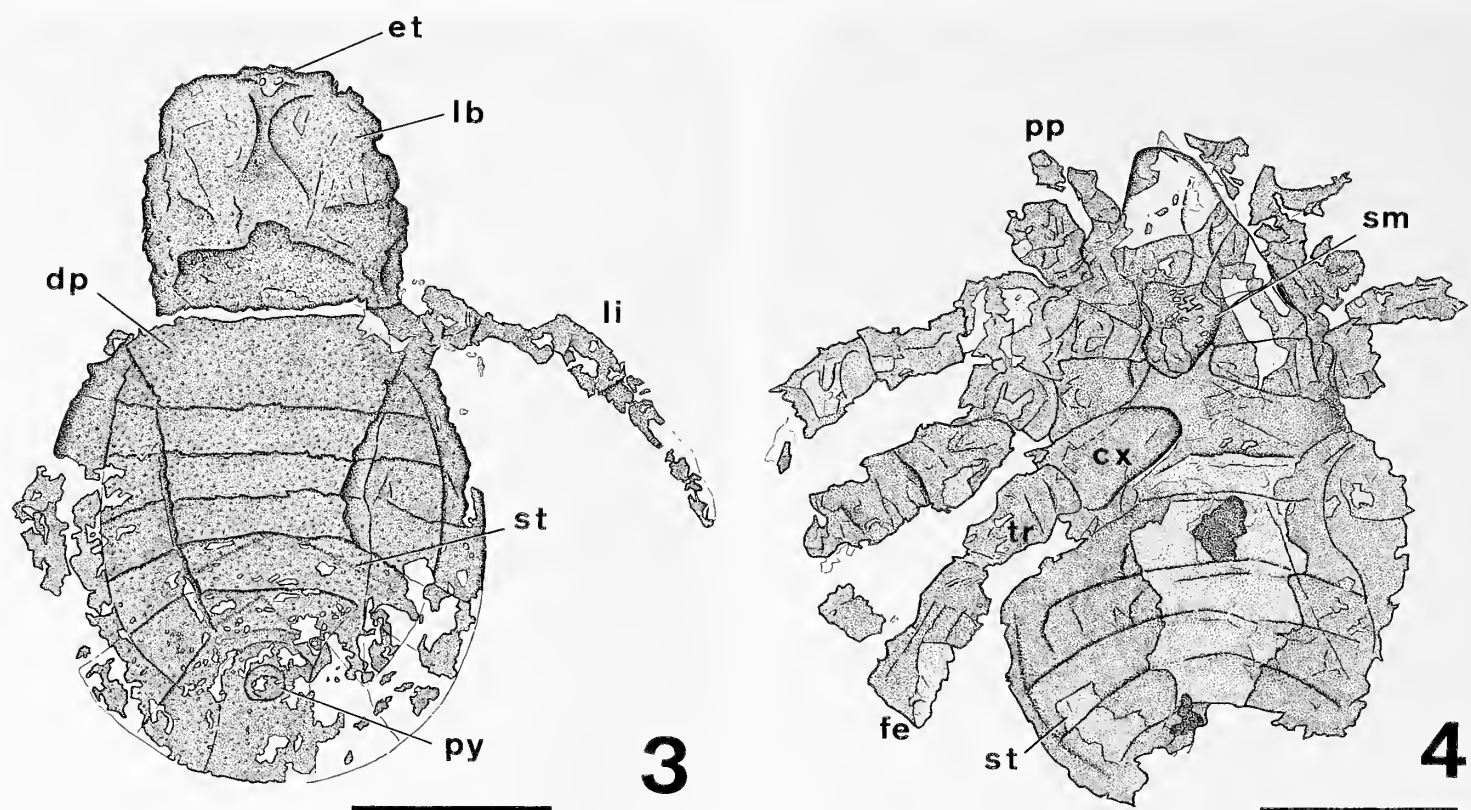
Anthracomartus völkelianus Karsch: Pocock 1911: 3–4, 63; Schwarzbach 1935: 5; Petrunkevitch 1949: 195–198, figs. 192, 193; Petrunkevitch 1953: 58, 68; Petrunkevitch 1955a: 107, fig. 67 (1).

Anthracomartus voelkelianus Karsch: Petrunkevitch 1913, pp. 94, 99.

Material.—BGR, Berlin No. 09446 (Holotype). From the 'Rubengrube', Nowa Ruda, Intra-Sudetic basin, Poland. Pennsylvanian (Langsettian). Not BGR, Berlin No. 09447 (see below).

Emended diagnosis.—Carapace with slightly bilobed anterior region divided by median sulcus. Opisthosoma broadly oval, almost circular in outline, but slightly longer than wide and widest midway along its length. Based on published descriptions, the opisthosoma of *A. granulatus* is wider than long.

Description.—Only carapace, opisthosoma and one leg preserved in dorsal view with



Figures 3–4.—Camera lucida drawings of the specimens shown in Figs. 1–2. Abbreviations: cx = coxa, et = probable median eye tubercle, fe = femur, lb = anterior lobe on carapace, li = limb, pp = pedipalp, py = pygidium, sm = sternum, st = sternites (superimposed through onto dorsal surface in Fig. 3), tr = trochanter. Scale = 5 mm.

some ventral features superimposed posteriorly (Figs. 1, 3). Total length 18.0. Whole specimen with a somewhat granular appearance, in places resolved into a distinct pattern of tiny tubercles. Carapace subquadrate, 6.1 long, 6.6 wide, slightly rounded at anterolateral corners. Carapace with slight relief, but margins on all sides irregular and full depth of carapace obscured within matrix. Carapace with somewhat bilobed appearance in anterior half; lobes approximately symmetrical. Posterior half of carapace somewhat depressed. Carapace lacks lateral eye tubercles and projecting anterior clypeus seen in more three-dimensionally preserved anthracomartids (Dunlop 1996; Dunlop & Horrocks 1996), but small, raised area near anterior margin consistent with median eye tubercle. Single, almost complete, but rather poorly preserved, leg occurs on right side, total length c. 9. Individual podomeres indistinguishable, probably leg IV judging from its position.

Opisthosoma broadly oval, slightly longer (11.7) than wide (11.2). Cuticle preserved as dark regions (best seen under alcohol) but preservation patchy in posterior region and towards margins of opisthosoma. Characteristic anthracomartid tergite pattern, including a large diplotergite (segments 2 + 3) and divi-

sion of most tergites into 5 plates with median plate wider than lateral plates, clearly visible, at least anteriorly. Posterior segmentation less distinct because ventral elements (sternites which are distinctly angled on the midline) are superimposed. Outline of circular pygidium (ventral, diameter 1.0) impressed through onto dorsal surface.

Remarks.—Karsch (1882) did not designate a type from among his ‘small number’ of specimens which implies a series of syntypes. However, since only two of these fossils have been positively identified, and since they appear not to be conspecific (see below), we regard the Berlin specimen corresponding to Karsch’s fig. 1 as the holotype; see also comments by Petrunkevitch (1949, p. 198). If more of the original Rubengrube material is subsequently identified and confirmed to be *A. voelkelianus* then BGR, Berlin No. 09446 may have to be redesignated as a lectotype.

An adequate diagnosis of both the genus and species is difficult without a revision of the anthracomartids and an assessment of the characters used to define taxa. Despite their apparent diversity in the literature, anthracomartid fossils are morphologically rather homogeneous. Furthermore, we are cautious about relying too heavily on reduction (e.g.,

absence of eyes or ornament) and/or proportion-based characters (e.g., length–width ratios) in material which has potentially been distorted during preservation. That said, provisional observations of other anthracomartid fossils suggest that gross morphological carapace ornamentation and the shape of the opisthosoma (i.e., circular, oval or pear-shaped) may be useful characters. This information has therefore been used in the diagnosis above.

Trigonotarbidæ Petrunkevitch 1949

?*Trigonotarb* sp. Pocock 1911

Figs. 2, 4

Anthracomartus Völkelianus Karsch 1882: 560–561, pl. 21, fig. 2.

Material.—BGR, Berlin No. 09447. From the Rubengrube, Nowa Ruda, Poland. Pennsylvanian (Langsettian). Reported counterpart (Geologisches Institut in Breslau [= Wrocław], No. 556) missing, presumed lost.

Description.—Incomplete specimen preserved in ventral view. Total preserved length 16.6. Prosoma subtriangular, converging to blunt point anteriorly. Mouthparts not preserved, but a series of subtriangular coxae, increasing in size from anterior to posterior, surrounds relatively large, heart-shaped sternal element. Proximal limb elements present, best preserved on left side, but incomplete. Pedipalps poorly preserved. All legs robust with somewhat rounded trochanters and short proximal podomeres; probably femora and patellae, although podomere boundaries mostly not clearly defined (Fig. 4). Opisthosoma incomplete, but preserved outline suggests it was almost circular (diameter c. 9.5.) in life; posterior, including pygidium, missing. At least five opisthosomal sternites visible, all lacking ornamentation and gently procurved with angle of procurvature increasing posteriorly.

Remarks.—As previous authors have hinted, this fossil cannot be the counterpart of 09446 (described above), nor is it conspecific with it. The proportions of the prosoma and opisthosoma, and of the appendages, are significantly different (compare Figs. 1 & 3 with 2 & 4). BGR 09447 cannot even be included in Anthracomartidae, a family which characteristically preserves a number of sharply angled ventral sternites in front of the pygidium (see also above; Fig. 2). The corresponding sternites in BGR 09447 are smoothly procur-

ved (Figs. 3, 4) and overall this fossil, with an apparently triangular prosoma ending in a bluntly rounded 'snout', is much more like examples of the family Trigonotarbidæ; compare with figures in Pocock (1911) and Petrunkevitch (1949, 1955b). BGR 09447 is tentatively referred to the genus *Trigonotarb*. In size and general shape BGR 09447 resembles the French Stephanian species *Trigonotarb arnoldi* Petrunkevitch 1955b, but since the Rubengrube fossil is only incompletely known from a rather poorly preserved ventral surface we are reluctant to assign it to a species.

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TASMABROCHUS, A NEW SPIDER GENUS FROM TASMANIA, AUSTRALIA (ARANEAE, AMPHINECTIDAE, TASMARUBRIINAE)

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ABSTRACT. Three species of *Tasmabrochus* new genus are described. The new species are *T. cranstoni* (type species), *T. montanus* and *T. turnerae*. They are placed with *Tasmarubrius* in a new subfamily Tasmarubriinae in the Amphinectidae.

Keywords: Taxonomy, Australia, new species, Gondwanan

The spiders here placed in the new genus *Tasmabrochus* were prominent among collections of Tasmanian spiders when describing *Tasmarubrius* (Davies 1998a). Before proceeding, I shall trace the history of *Amphinecta* Simon 1898 and the Amphinectidae. *Amphinecta* was described from New Zealand (type species *A. decemmaculata* Simon 1898) and placed in the Agelenidae. Lehtinen (1967) transferred it to the Amaurobiidae: Desinae and at the same time placed *Rubrius milvinus* Simon 1903 from Tasmania into a new combination, *Amphinecta milvina*. Forster & Wilton (1973) raised *Amphinecta* to a new family, the Amphinectidae, which comprised sixteen genera from New Zealand, thirteen of which were new. They dismissed Lehtinen's view that the Tasmanian spider *A. milvina* belonged in *Amphinecta* or the Amphinectidae. Davies (1998a) placed the Tasmanian *R. milvinus* in the genus *Tasmarubrius* and assigned it to the Amaurobiidae. However a recent cladistic analysis (Davies & Lambkin 2001) which included the type species of *Amaurobius*, *A. fenestralis* (Ström 1768) from Europe, among Australasian exemplars found the placement of *Amaurobius* ambiguous. In half (eighteen) of the MPTs it formed a third basal clade with *Badumna* (Davies & Lambkin 2001, fig. 10) while in the other half it was sister to a large clade that did not include *Tasmarubrius*. Thus *Tasmarubrius* is here provisionally transferred to its most closely related family, Amphinectidae.

The Metaltellinae is also considered a subfamily of the Amphinectidae. Lehtinen (1967)

considered it a subfamily of the Amaurobiidae. It is a well defined group of genera found in South and Central America and in Australia. Davies (1998b) placed it in the Amphinectidae as the closest available family in the cladistic analysis. This was supported by Griswold et al. (1999) in their analysis of the cribellate entelegyne spiders. In their cladogram *Maniho* Marples 1959, the amphinectid exemplar and *Metaltella* Mello-Leitão 1931 were a sister group to the Desidae.

A new subfamily Tasmarubriinae is established for the reception of *Tasmarubrius* and the new genus described here, *Tasmabrochus*. It is interesting to note that Churchill (1993: 477) listed the male as *Mamoea* sp., an amphinectid from New Zealand and the female as 'gen. A sp.2'. As there is no clear diagnosis of the family Amphinectidae, the subfamily will be compared with the type genus, *Amphinecta*.

METHODS

Nearly all of the collection was from pit-fall (PF) trapping in both the coastal heathland of north-eastern Tasmania and in the north-western highlands region. Notation of spines follows Platnick & Shadab (1975); measurements are in millimeters; the left male palp is used in illustrations. The usual abbreviations are used for body length, eyes, spinnerets and spigots. Abbreviations on figures are explained in the legend.

Specimens are deposited in the following museums: Queen Victoria Museum, Launceston, Tasmania (QVM), Tasmanian Museum,

Hobart, Tasmania (TM) and Queensland Museum, Brisbane, Queensland (QM).

SYSTEMATICS

Tasmarubriinae new subfamily

Diagnosis.—Like *Amphinecta*, the *tasmarubriinae* are three-clawed ground living ecribellates found under logs and rocks. They share the following characters: geniculate chelicerae with two retromarginal teeth; cuticle ridged and without feathery hairs; preening combs present distally on some metatarsi; small membranous conductor; movable median apophysis and a distal RTA and dorso-retrolateral apophysis. They differ from *Amphinecta* in the division of the tegulum into proximal and distal parts, a short thick embolus, simple insemination ducts and cymbial apophyses. In contrast, *Amphinecta* has a long, coiled spiniform embolus, loosely coiled insemination ducts and lacks cymbial apophyses.

Description.—Reddish brown carapace, almost glabrous; dark brown abdomen with indistinct pattern of six pairs of pale spots, venter pale mottled with brown. From above, posterior eye row procurved (Fig. 2), anterior row slightly so; from the front both rows strongly procurved. AME reduced. Geniculate chelicerae (Fig. 1) with two retromarginal and two promarginal teeth (Fig 4). Sternum longer than wide, pointed posteriorly. Legs 4123: all tibiae and metatarsi have paired ventral spines which are longer on the posterior legs. Single row of trichobothria on metatarsi and tarsi; tarsal organ slit-like (Fig. 12). Epigynum with lateral gonopores. Tegulum of male palp with proximal and distal divisions, the latter bearing a short thick embolus, a small membranous conductor, a large movable elongate median apophysis and usually a fixed tegular apophysis. Cymbium with small bulge on retrolateral edge and proximal projection (paracymbium). Palpal tibia with large retrolateral excavation with ventro-and dorso-retrolateral branches. Small D-shaped colulus. Two major ampullate spigots on ALS, the anterior larger than the posterior; the latter reduced to a nubbin in male.

Tasmabrochus new genus

Type species.—*Tasmabrochus cranstoni* new species.

Etymology.—The generic name is a combination of 'Tasma' from Tasmania and Latin 'brochus', a projection, referring to the very prominent tegular apophysis of the male palp. It is considered masculine in gender.

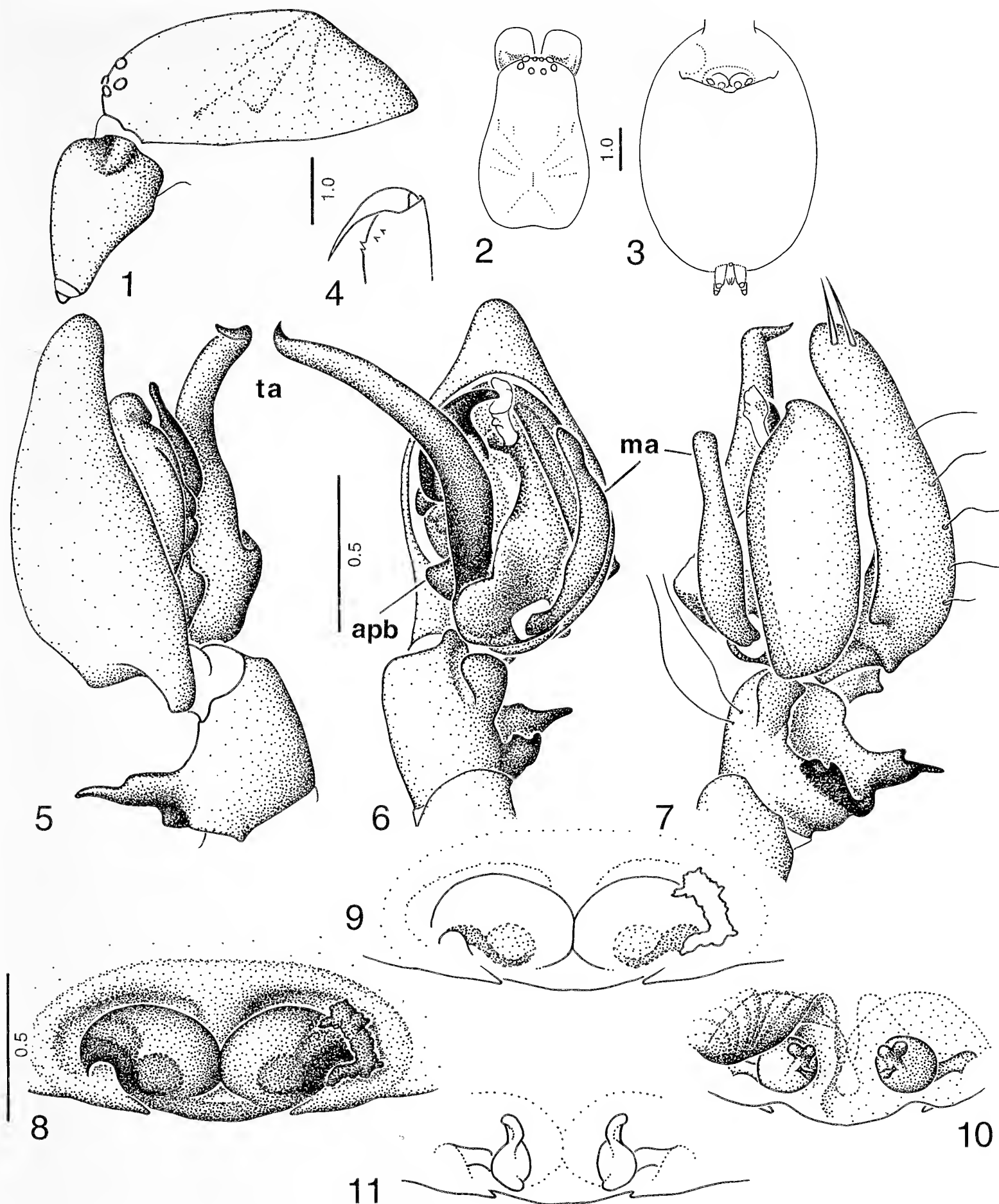
Diagnosis.—Members of the genus resemble *Tasmarubrius* in having two retromarginal and two promarginal cheliceral teeth, and a large fixed tegular apophysis and cymbial apophyses in the male. *Tasmabrochus* differs from *Tasmarubrius* in having lateral teeth on the epigynum and lacking lateral epigynal protuberances. The long fixed tegular apophysis is in a ratio of 1:0.7 to the median apophysis whereas they are about equal (1:0.9) in *Tasmarubrius*. Cymbium with small retrolateral paracymbium and a posterior prolateral extension whereas *Tasmarubrius* has a large paracymbium and lacks prolateral extension. Preening combs on metatarsi III and IV, absent on II; whereas they are present on II, III and IV in *Tasmarubrius*.

Tasmabrochus cranstoni new species

Figs. 1–13, 15–19, Table 1

Types.—**Australia: Tasmania.** Holotype male, dry sclerophyll, Peters Link Rd, NE Tasmania, 41°08'S, 148°07'E, PF, site B2.2, 22–27 May 1993, P. Cranston, J. Trueman (QM S42321). Paratypes: 1 ♀, same locality, date, collectors as holotype, site B1.2 (QM S42322); 2 ♂, as above, site B1.1 (QM S42323); 1 ♂, site B1.2 (QM S42324); 1 ♂, site B2.1 (QM S42325); 1 ♀, site B3.2 (QM S42326); 1 ♀, site B5.1 (QM S42327); 1 ♂, coastal heath, Eddystone Pt. 41°00'S, 148°19'E, PF, site C4.1, 22–27 May 1993, P. Cranston, J. Trueman (QM S42328); 1 ♂, same locality and collectors, site C3.2, 23–28 Aug.1993 (QM S42329); 1 ♂, C4.1, 23–28 Aug.1993 (QM S42330); 1 ♂ C4.2 (QM S42331); ♂, *Leptospermum* wet heath, Anson's Bay Rd, 41°02'S, 148°14'E, site D2.1, 23–28 Aug.1993, P. Cranston, J. Trueman (QM S42332); 2 ♀, in regeneration area, old Chum Dam, 10–15 km NE Pioneer; 41°03'S, 148°01'E, 200m, PF, October 1989–April 1990, Forestry Department (TM J3260); 4 ♂, as above (TM J3261); 1 ♂, Freycinet NP, 42°09'S, 148°18'E, eucalypt forest, 27 May 1996, J. Boutin (TM J3265); 1 ♀, Gray, rotting log on dry hillside, 41°38'S, 148°13'E, 13 Aug. 1974, R. Mesibov (TM J3308).

Etymology.—The specific epithet is a pa-



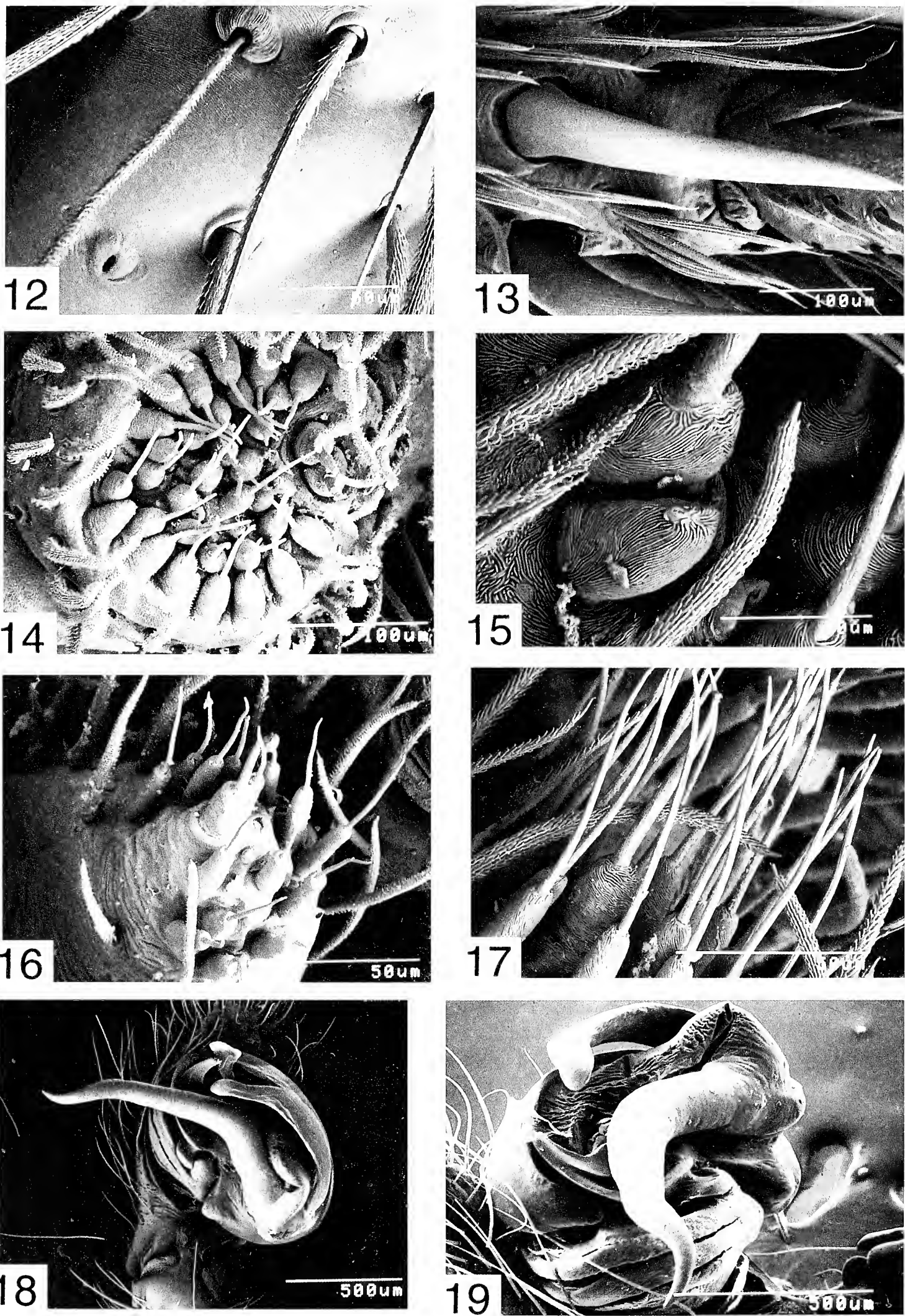
Figures 1–11.—*Tasmabrochus cranstoni* new species. 1, 2. Female carapace. 1, Lateral; 2, Dorsal. 3, Abdomen, ventral. 4, Chelicera, ventral. 5–7, Male palp. 5, Prolaterodorsal. 6, Ventral. 7, Retrolateral. 8–11, Epigynum. 8, Dorsal. 9, Dorsal cleared. 10, Ventral. 11, Posteroventral. *Abbreviations*: apb: angular prolateral bulge; ma, median apophysis; ta, tegular apophysis.

tronym in honor of Dr. Peter Cranston, one of the collectors of the holotype.

Diagnosis.—Males can be recognized by the angular bulge on the prolateral tegulum

(Fig. 6) and the blunt prolongation of posterior prolateral cymbium (Fig. 5).

Description.—Male: CL 3.8, CW 2.5, AL 3.7, AW 2.1. Pale cardiac patch on abdomen,



Figures 12–19.—12, 13, 15–19, Male *Tasmabrochus cranstoni* new species. 12, Tarsal organ and tri-chobothrium, leg I; 13, Two preening combs distal to spine, metatarsus III; 15, ALS (l) with one MAP and nubbin; 16, PMS (l) with mAP; 17, PLS (r) with large spigot among aciniforms; 18, Palp, ventral; 19, Palp, prolateral. 14, Female *Tasmarubrius turnerae* new species, ALS (r) with two MAP medially.

Table 1. Leg lengths of male (female) *Tasmabrochus cranstoni* new species.

	I	II	III	IV
Femur	2.8 (3.0)	2.5 (2.5)	2.2 (2.2)	2.8 (3.0)
Patella and tibia	3.8 (3.8)	3.0 (3.3)	2.6 (2.8)	3.8 (3.8)
Metatarsus	2.6 (2.1)	2.2 (2.0)	2.4 (2.3)	3.4 (2.9)
Tarsus	1.6 (1.2)	1.2 (1.0)	1.0 (1.0)	1.3 (1.1)
Total	10.8 (10.1)	8.9 (8.8)	8.2 (8.3)	11.3 (10.8)

venter mottled. Ratio of AME: ALE: PME: PLE is 5:9:7:9. Labium about as wide as long; sternum longer than wide. Legs 4123 (Table 1). Notation of spines. Femora: I, D110, P002; II, D110, P001; III D110, P001, R001; IV, D110, P001, R001. Tibiae: I, P111, V222; II, P111, V122; III D010, P111, V212, R201; IV, D010, P111, V212, R111. Metatarsi: I, P012, V221, R001; II P112, V221, R012; III, D111, P212, V221, R211; IV, D110, P212, V221, R212. Preening combs (Fig. 13) on metatarsi III (two with 4 tines each), IV (two with 4 tines). Palp (Figs. 5–7, 18,19) small membranous conductor; broad spatulate median apophysis, slightly bowed; very long tegular apophysis extending well beyond tegulum; heavily sclerotised blunt embolus. Angular prolateral bulge on tegulum. Blunt projection on posterior prolateral cymbium. Tibial apophysis deeply excavated with sharp dorso-retrolateral spur. Spinnerets (Figs. 15–17) ALS with one major ampullate gland spigot and a nubbin; about 15 piriform spigots. PMS with one large minor ampullate spigot and about 15 small aciniform spigots. PLS with one large spigot and more than 20 aciniforms. Males varied in length between 6.6–7.8.

Female: CL 4.3, CW 2.9, AL 6.5, AW 4.5. Ratio of AME: ALE: PME: PLE is 6:9:8:10. Labium about as wide as long; sternum longer than wide, 1:09. Legs 4123 (Table 1). Notation of spines. Femora: I, D110, P001; II, D110, P001, III D110, P001, R001; IV, D110, P001, R001. Tibiae: I, V222; II V122; III, D010, P111, V212, R101; IV, D001, P111, V212, R111. Metatarsi: I, P001, V221, R001; II, P012, V221, R011; III, D100, P112, V221, R112; IV, D110, P112, V221, R112. Preening combs on metatarsi III and IV as in male. Epigynum (Figs. 8–11) small, about a tenth the length of venter (Fig. 3); irregular shaped plugs in some gonopores. Small colulus with 4 setae. Spinnerets: ALS with two major ampullate gland spigots, the anterior larger than

posterior, about 25 piriforms. PMS with one large minor ampullate spigot.

Females varied in length between 7.5–10.8.

Tasmabrochus montanus new species
Figs. 20–24, 28, 29

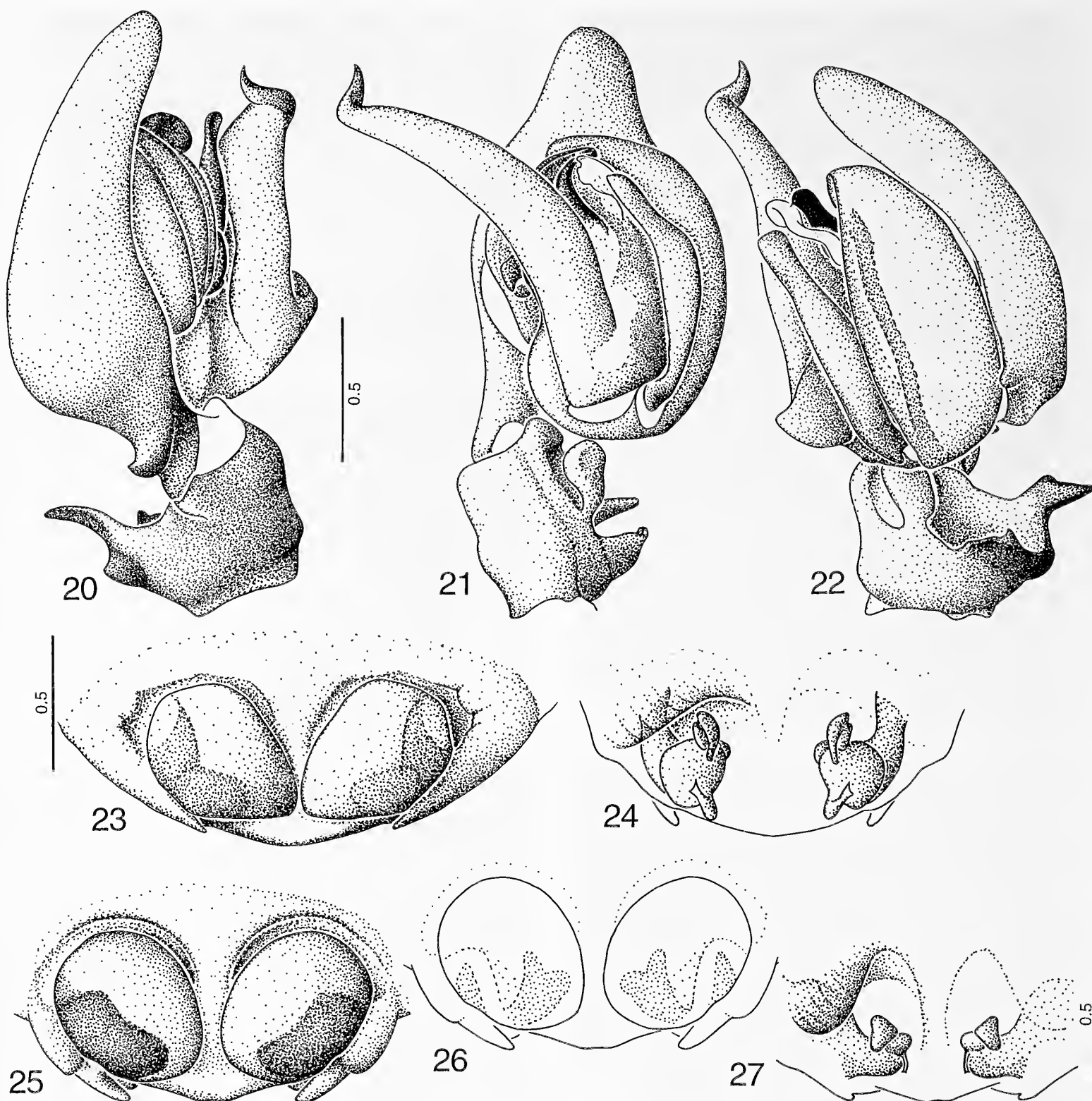
Types.—Australia: Tasmania. Holotype male, Maggs Mt, NW Tasmania, 41°45'S, 146°12'E, PF, 13 June–19 September 1979, R.H. Green (QVM 25951). Paratypes: 1 ♀, same data as holotype (QVM 25952); 45 ♂, same data as holotype (QVM 25953); 34 ♀, same data as holotype (QVM 25954); 2 ♀, 1 ♂, same locality and collector, 12 May 1980 (QVM 25955); 4 ♂, 4 ♀ (QVM:13:7074)

Etymology.—The specific epithet is from Latin 'montanus', mountain, for the type locality, Maggs Mountain.

Diagnosis.—Females very similar to *T. cranstoni*. Males can be recognised by the smooth rounded prolateral tegulum (Fig. 21) and the sharp point on the posterior prolateral cymbium.

Description.—Male: CL 4.0, AL 3.8. Coloration and pattern are similar to *T. cranstoni*. Ratio of AME: ALE: PME: PLE is 7:10:8:9. Legs 4123. I 12.3; II 10.2; III 9.7; IV 12.9. Notation of spines and preening combs similar to *T. cranstoni*. Male palp (Figs. 20–22) without angular prolateral bulge on tegulum (Fig. 21). Sharp point on posterior prolateral cymbium (Fig. 20). Males varied in length between 6.4–7.9.

Female: CL 4.6, AL 6.6. Legs: I 11.9; II 9.3; III 9.1; IV 12.5. Coloration, eyes, notation of spines similar to *T. cranstoni*. Epigynum (Figs 23–24, 28) about one tenth length of venter. PMS (Fig. 29) with a large minor ampullate spigot, two cylindrical spigots (one ectal, one posterior) and about sixteen smaller aciniform spigots. Females varied in length between 8.8–11.2.



Figures 20–27.—20–24, *Tasmabrochus montanus* new species. 20–22, Male palp. 20, Prolateral. 21, Ventral. 22, Retrolateral. 23, 24, Epigynum. 23, Ventral. 24, Dorsal. 25–27, *Tasmabrochus turnerae* new species, epigynum. 25, Ventral. 26, Ventral cleared. 27, dorsal.

Tasmabrochus turnerae new species

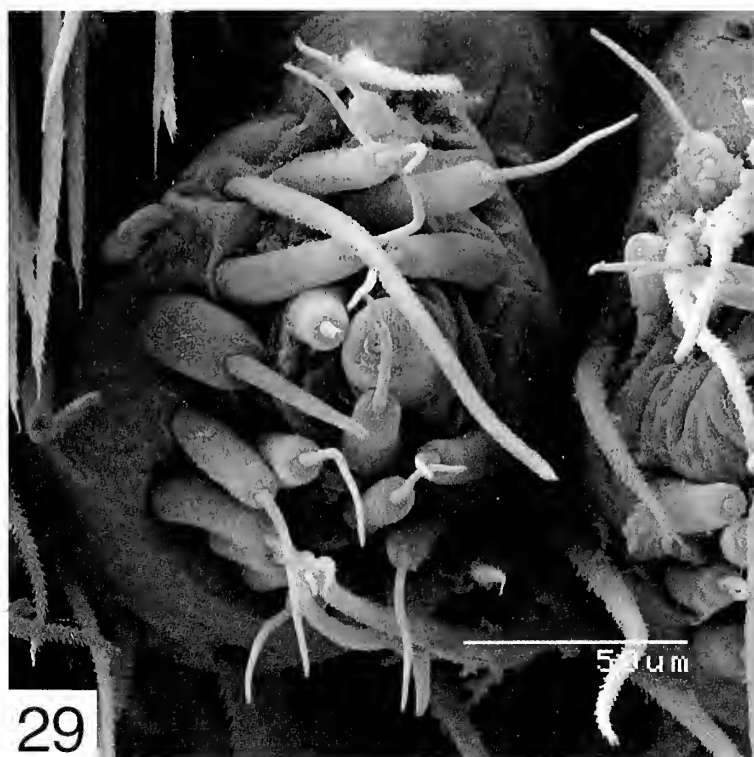
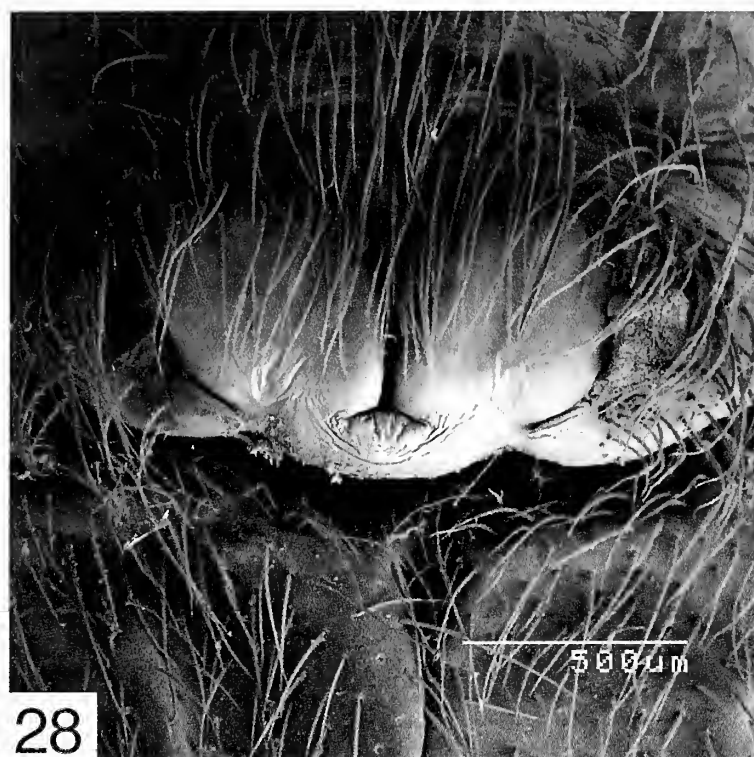
Figs. 14, 25–27

Types.—**Australia: Tasmania.** Holotype female, under rock at helipad, lower summit of Mt Maria, Maria I, SE Tasmania, 42°37'S, 148°06'E, 680 m, 6 March 1990, E. Turner (TM J2944). Paratypes: 3 ♀, same data as holotype (TM J3266).

Etymology.—The specific epithet is a patronym in honor of Elizabeth Turner, Curator of Zoology at the Tasmanian Museum and collector of these specimens.

Diagnosis.—Females may be recognised by the speckled brown abdomen with dark brown cardiac area. Epigynum about a sixth the length of venter compared with a tenth in other species; smaller storage area of spermatheca than in other species.

Description.—Female: CL 5.0, CW 3.3 AL 5.4, AW 3.2. Carapace dark reddish brown; abdomen with dark brown cardiac stripe and indistinct paired pale patches; pale venter with dark brown mottling. Ratio of eyes AME: ALE: PME: PLE is 8:11:9:11. Labium slightly longer than wide; sternum longer than wide 1:



Figures 28, 29.—*Tasmabrochus montanus* new species. 28, Epigynum, ventral; 29, PMS (shaft of large minor ampullate spigot is broken off).

0.8. Legs 4123. I 13.1; II 11.5, III 10.8; IV 14.5. Notation of spines. Femora: I, D110, P002; II, D110, P001; III, D110, P001, R001; IV, D110, P001, R001. Tibiae: V222; II, V112; III, D010, P111, V212, R111; IV, D001, P111, V212, R111. Metatarsi: I, P001, V221, R001; II P012, V221, R001; III, D110, P212, V221, R212; IV, D110, P212, V221, R212. Preening combs on metatarsi III (two with 6 & 5 tines each), IV (two with 6 & 5 tines). Epigynum (Figs. 25–27) about a sixth the length of the venter; small storage area in spermathecae. Spinnerets: ALS with two major ampullate spigots and about 25 piriform spigots (Fig. 14). PMS and PLS with one large spigot and smaller spigots. Colulus with about 10 setae. Females varied in size between 9.5–11.0.

Male: Unknown.

ACKNOWLEDGMENTS

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illustrator, Christine Lambkin. I also thank Kylie Stumkat and Jane Christensen, scanning electron microscope technicians, and other staff of the Queensland Museum, particularly Christine Thai for their help in preparation of this paper.

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A PRELIMINARY MOLECULAR ANALYSIS OF PHYLOGENETIC RELATIONSHIPS OF AUSTRALASIAN WOLF SPIDER GENERA (ARANEAE, LYCOSIDAE)

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ABSTRACT. A data-set from the mitochondrial 12S rRNA gene subunit of 11 Australasian lycosid species (six New Zealand species and five Australian species) was generated. Three North American lycosid species, one European species and one New Zealand pisaurid (outgroup) were also sequenced. The sequence data for the 16 species were combined with the published sequences of 12 European lycosids, two Asian lycosids and one Asian pisaurid and were analyzed using parsimony and maximum likelihood analyses. The resulting phylogenetic trees reveal that Australasian species largely form clades distinct from Palearctic and Holarctic species providing further evidence against the placement of Australasian species in Northern Hemisphere genera. New Zealand wolf spiders appear to be related to a subset of Australian genera whereas the other Australian lycosid genera are related to Asian/Holarctic faunas. Gene sequences in the 12S region were useful when examining relationships between closely related genera, but were not as informative for deeper generic relationships.

Keywords: Lycosidae, New Zealand, Australia, lycosid genera, lycosid subfamilies

The monophyly of the Lycosidae is well supported (e.g. Dondale 1986; Griswold 1993), but at the subfamily level there is some disagreement (Dondale 1986; Zyuzin 1993; Dippenaar-Schoeman & Jocqué 1997) and lycosid genera, many of which are paraphyletic and polyphyletic, are in disarray. Although European lycosid generic placements are well established (e.g. Heimer & Nentwig 1991) and some Nearctic and African genera have been recently revised (e.g. Alderweireldt 1991, 1999; Dondale & Redner 1978, 1979, 1983a, 1983b; Russell-Smith 1982), a large number of the 2245 lycosid species (Platnick 2001) would seem to be misplaced. For example, a revision of the New Zealand lycosid fauna (Vink 2002) found that all but one described species were incorrectly placed in mostly Northern Hemisphere genera. Some of the confusion can be attributed to Roewer (1951, 1955, 1959, 1960) who described 65 lycosid genera of which only 31 are currently recognized (Platnick 2001); 12 of these are monotypic and many others contain only two species. Roewer's generic descriptions were short and based on highly variable, non-genitalic characters. Brignoli (1983) stated "it is apparent that most recent students of this

group give little value to most of the genera described by Roewer in 1954 [1955] and 1960; still it is necessary to list them as no acceptable new 'system' has been yet proposed". However, Roewer cannot be held entirely responsible for the state of lycosid genera. Many of the generic problems are due to the morphological conservatism of the Lycosidae and the consequential lack of useful characters to define and separate genera.

In New Zealand and Australia, many early workers placed lycosid species into genera with which they were familiar in their native Europe (e.g. Koch 1877). In particular, *Lycosa* Latreille 1804, which is now considered to be a Mediterranean genus (Zyuzin & Logunov 2000), has been a convenient genus in which to place many new species or as a temporary home when genera need revising (e.g. McKay 1975). Many of the large, burrow-dwelling Australian species have been placed in *Lycosa* (e.g. *Lycosa godeffroyi* L. Koch 1865) but do not fit the genus as defined by Zyuzin & Logunov (2000). Rather, they have a genitalic morphology similar to *Geolycosa* Montgomery 1904 (sensu Dondale & Redner 1990).

Lycosids are among the numerically dominant arthropod predators found in open habi-

tats in Australasia (e.g. Forster 1975; Humphreys 1976; Churchill 1993; Sivasubramaniam et al. 1997; Hodge & Vink 2000; Framenau et al. 2002) and recent taxonomic work (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002) has addressed the generic placement of some Australasian species. New Zealand's fauna, comprising 27 species, has been revised (Vink 2002) with most species (20) in *Anoteropsis* L. Koch 1878. The Australasian genera *Allotrochosina* Roewer 1960 (two species), *Artoria* Thorell 1877 (17 species), *Notocosa* Vink 2002 (one species) and *Venatrix* Roewer 1960 (22 species) have been recently revised or reviewed (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002). There are also 12 Australian species that form "a natural grouping" and were placed in *Trochosa* C.L. Koch 1848 (McKay 1979) but none of these species fit the genus as defined by Dondale & Redner (1990). Australia has 141 described lycosid species and at least another 100 undescribed species (V.W. Framenau pers. comm.; CJV pers. obs.). The majority of Australian species appear to belong in *Artoria* and a *Geolycosa*-like genus (V.W. Framenau pers. comm.; CJV pers. obs.). Species in *Venatrix* and the *Geolycosa*-like genus have a pedipalpal configuration that places them in the Lycosinae Simon 1898 (Framenau & Vink 2001; CJV pers. obs.). Vink (2001) placed *Allotrochosina* in Venoniinae Lehtinen & Hippa 1979 (sensu Dondale 1986) and while the simple pedipalps of *Anoteropsis*, *Artoria*, *Notocosa* and the Australian species currently in *Trochosa* do not fit any of the current subfamily definitions (Framenau 2002; Vink 2002; CJV pers. obs.) they are perhaps closest to Venoniinae (sensu Dondale 1986). The phylogenetic position of Australasian genera within the Lycosidae is unknown.

Because lycosids are morphologically conservative it is unlikely that sufficient numbers of morphological characters could be found to infer phylogenetic relationships of Australasian genera to their counterparts in the rest of the world. Sequence data from a portion of the mitochondrial 12S rRNA gene of the small ribosomal subunit have yielded large data sets for phylogenetic analysis of spiders (e.g. Gillespie et al. 1994). Recently, 12S rRNA sequence data have been used to infer relationships among European lycosids (Zehethofer & Sturmbauer 1998; Vink & Mitchell 2002) and

the relationship of Asian lycosids to other Lycosoidea (Fang et al. 2000). Zehethofer & Sturmbauer (1998) found that 12S rRNA was especially suitable for resolving relationships higher than the species level.

This preliminary study aimed to examine the relationship of exemplars of the major Australasian genera to exemplars of genera found elsewhere in the world using phylogenetic analyses of 12S rDNA sequence data.

METHODS

Generic placement of species was based on the latest catalog of Platnick (2001) and recent taxonomic revisions (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002). Species sequenced, sex, and collection details (locality, date and collectors) are shown in Table 1. All specimens are stored in 95% ethanol and refrigerated in the Ecology & Entomology Group, Lincoln University. Selected Australasian species represented the major species groups of Australia and New Zealand (Framenau 2002; Framenau & Vink 2001; Vink 2001, 2002; CJV pers. obs.). The North American species *Geolycosa rogersi* Wallace 1942, *Varacosa avara* (Keyserling 1877) and *Allocosa georgicola* (Walckenaer 1837) were sequenced and included in the analysis because of the similarity of their male pedipalp morphology to *Lycosa godeffroyi*. It should be noted that *Allocosa georgicola* does not fit the genus *Allocosa* Banks 1900 as defined by Dondale & Redner (1983b).

DNA extraction, amplification and sequencing.—Specimens were washed in sterile deionized, distilled water before DNA extraction. Total genomic DNA was extracted by homogenizing 1–2 legs from single individuals (Table 1) using a proteinase-K digestion and high salt precipitation method (White et al. 1990). Mitochondrial 12S regions were amplified using the following two primer combinations:

- 1) 12St-L (5'-GGTGGCATT TTTATTTTAT-TAGAGG-3') (Croom et al. 1991) plus 12Sbi-H (5'-AAGAGCGACGGGCGATGTGT-3') (Simon et al. 1990), or
- 2) 12SR-N-14594 (5'-AAACTAGGATTAGATACCC-3') plus 12SR-J-14199 (5'-TACTATGTTACGACTTAT-3') (Kambhampati & Smith 1995) (Fig. 1).

Each 25 µl reaction consisted of 1× *Taq*

Table 1.—Specimens sequenced showing species, sex, collection localities, collectors and dates collected, primers used and GenBank accession numbers.

Species	Sex	Collection details	Primers used	GeneBank accession no.
<i>Allocosa georgicola</i> (Walckenaer 1837)	female	USA, near Oxford (34°13'N, 89°19'W), 12.x.1999, L. Schaffer	12SR-J + 12SR-N	AF380499
<i>Alopecosa barbipes</i> (Sundevall 1833)	male	England, Redgrave & Lopham Fen (52°23'N, 01°00'E), 6.x.1999, C.J. Vink & M.A. Hudson	12St-L + 12Sbi	AY028420
<i>Allotrochosina schauinslandi</i> (Simon 1899)	female	New Zealand, Prices Valley (43°48'S, 172°41'E), 12.vi.1999, C.J. Vink & J.W. Griffiths	12St-L + 12Sbi	AF380502
<i>Anoteropsis adumbrata</i> (Urquhart 1887)	female	New Zealand, Titan Rocks (45°32'S, 169°00'E), 9.xii.1998, G. Hall, B. Brown & E. Edwards	12St-L + 12Sbi	AF380491
<i>Anoteropsis lacustris</i> Vink 2002	male	New Zealand, Arthur's Pass (42°56'S, 171°34'E), 9.iv.1999, C.J. Vink & M.A. Hudson	12St-L + 12Sbi	AF380489
<i>Anoteropsis senica</i> (L. Koch 1887)	male	New Zealand, Franz Josef Glacier (43°25'S, 170°10'E), iv.1999, C.J. Vink & M.A. Hudson	12SR-J + 12SR-N	AF380490
<i>Artoria flavimanus</i> Simon 1909	male	Australia, Crowea (34°28'S, 116°10'E), 6.v.1999, C.J. Vink	12SR-J + 12SR-N	AF380492
<i>Dolomedes minor</i> L. Koch 1876	female	New Zealand, Lake Ellesmere (43°43'S, 172°30'E), 20.xi.1999, R.M. Emberson	12SR-J + 12SR-N	AF380503
<i>Geolycosa rogersi</i> Wallace 1942	female	USA, Avent Park 34°13'N, 89°18'W), 1.iv.2000, G. Stratton, P. Miller & B. Suter	12SR-J + 12SR-N	AF380498
<i>Lycosa godeffroyi</i> L. Koch 1865	female	Australia, Bellerive (42°52'S, 147°22'E), 11.v.1999, C.J. Vink & J. Cossum	12SR-J + 12SR-N	AF380497
<i>Notocosa bellicosa</i> (Goyen 1887)	male	New Zealand, Temuka (44°14'S, 171°17'E), iii.1999, M. Ross	12SR-J + 12SR-N	AF380493
<i>Trochosa oraria</i> (L. Koch 1876)	female	Australia, Lauderdale (42°55'S, 147°29'E), 11.v.1999, C.J. Vink & J. Cossum	12St-L + 12Sbi	AF380501
<i>Varacosa avara</i> (Keyserling 1877)	male	USA, Sardis Reservoir (34°15'N, 89°28'W), 14.ix.1999, G. Stratton & W. Calvert	12SR-J + 12SR-N	AF380500
<i>Venatrix goyderi</i> (Hickman 1944)	female	New Zealand, near Matarau (35°38'S, 174°11'E), 15.ii.1999, C.J. Vink	12St-L + 12Sbi	AF380496
<i>Venatrix lapidosa</i> (McKay 1974)	male	Australia, Avon River (37°48'S, 146°57'E), iii.1999, V.W. Framenau	12SR-J + 12SR-N	AF380495
<i>Venatrix pictiventris</i> (L. Koch 1877)	male	Australia, Queens Domain (42°52'S, 147°19'E), 9.v.1999, C.J. Vink	12St-L + 12Sbi	AF380494

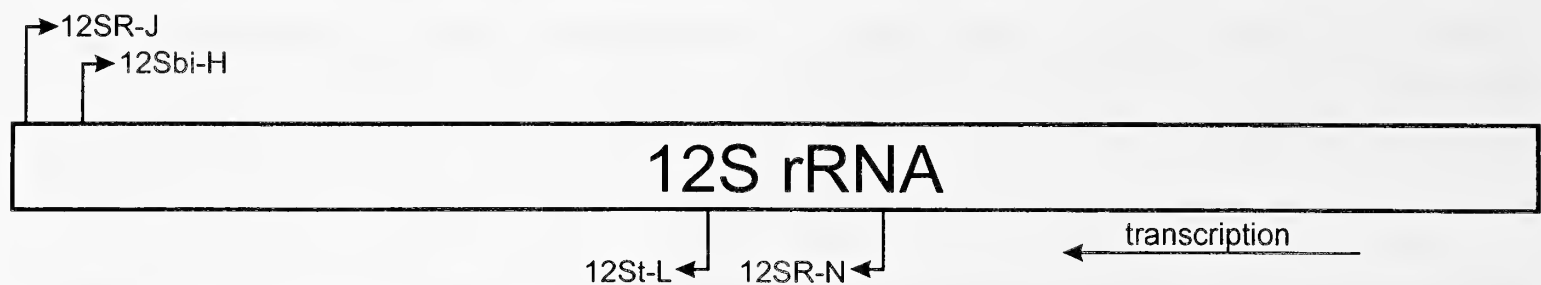


Figure 1.—Gene region coding for 12S rRNA showing areas sequenced by primers and direction of transcription.

buffer, 0.25 mM dNTPs, 2 mM MgCl₂, 0.4 μM of each primer, 1.25 units *Taq* DNA Polymerase (Roche) and 1 μl of genomic DNA [which was diluted 1:20 in TE (10 mM Tris, 1 mM EDTA, pH 8.0) and used as a template for the amplification of double-stranded DNA (dsDNA)]. Amplification was performed in a GeneAmp® PCR System 2400 (Perkin–Elmer) thermocycler and the following temperature profile was used: 4 min. at 94 °C; 40 cycles of 20 s at 94 °C, 30 s at 50 °C, 40 s at 72 °C; 2 min. at 72 °C. Excess primers and salts were removed from the resulting dsDNA by precipitation with 100% isopropanol in the presence of 2.5M NH₄Ac, followed by a 70% ethanol wash. Purified PCR fragments were sequenced using ABI PRISM® BigDye™ termination mix version 1 (Perkin-Elmer) and separated on an ABI PRISM® 373 automatic sequencer. The sense and antisense strands were sequenced for all species except *Venatrix pictiventris* L. Koch 1877 and *Anoteropsis la-*

custris Vink 2002, which were successful only one way. Sequence data were deposited in GenBank (Benson et al. 2000) (see Table 1 for accession numbers).

Data analysis.—Sequences were aligned to 15 previously published sequences (Zehethofer & Sturmbauer 1998; Fang et al. 2000) (Table 2) using Clustal W 1.7 (Thompson et al. 1994), then confirmed by eye. Insertion/deletion events were inferred where necessary based on the secondary structure of 12S rRNA proposed by Hickson et al. (1996). Although Hickson et al. (1996) used the 12S sequence of *Tetragnatha mandibulata* Walckenaer 1842 when constructing their template, helix 42 did not seem to be present in the lycosid or pisaurid sequences. In order to match the data obtained by Zehethofer & Sturmbauer (1998) sequence data that began five bases downstream from where the 12St-L primer annealed to seven bases upstream from where the 12Sbi-H primer annealed were included in

Table 2.—Other published sequences used in analyses showing species, reference and Genebank accession numbers.

Species	Reference	GenBank accession no.
<i>Alopecosa accentuata</i> (Latreille 1817)	Zehethofer & Sturmbauer (1998)	AJ008022
<i>Alopecosa pulverulenta</i> (Clerck 1757)	Zehethofer & Sturmbauer (1998)	AJ008025
<i>Arctosa leopardus</i> (Sundevall 1833)	Zehethofer & Sturmbauer (1998)	AJ008032
<i>Dolomedes raptor</i> Bösenberg & Strand 1906	Fang et al. (2000)	AF145031
<i>Lycosa coelestis</i> L. Koch 1878	Fang et al. (2000)	AF145030
<i>Pardosa agrestis</i> (Westring 1861)	Zehethofer & Sturmbauer (1998)	AJ008033
<i>Pardosa hortensis</i> (Thorell 1872)	Zehethofer & Sturmbauer (1998)	AJ008007
<i>Pardosa palustris</i> (Linnaeus 1758)	Zehethofer & Sturmbauer (1998)	AJ008011
<i>Pardosa takahashii</i> (Saito 1936)	Fang et al. (200)	AF145032
<i>Pirata hygrophilus</i> Thorell 1872	Zehethofer & Sturmbauer (1998)	AJ008015
<i>Pirata knorri</i> (Scopoli 1763)	Zehethofer & Sturmbauer (1998)	AJ008019
<i>Trochosa terricola</i> Thorell 1856	Zehethofer & Sturmbauer (1998)	AJ008017
<i>Trochosa spinipalpis</i> (F.O.P.-Cambridge 1895)	Zehethofer & Sturmbauer (1998)	AJ008016
<i>Xerolycosa miniata</i> (C.L. Koch 1834)	Zehethofer & Sturmbauer (1998)	AJ008021
<i>Xerolycosa nemoralis</i> (Westring 1861)	Zehethofer & Sturmbauer (1998)	AJ008020

the analyses. The analyses were conducted using PAUP* 4.0b4a (Swofford 2000).

Data were analyzed as unordered characters, first using parsimony and the heuristic search (1000 replicates) option in PAUP*. All characters were equally weighted, and zero length branches were collapsed to polytomies. Bootstrap values (Felsenstein 1985) were calculated from 1000 replicate parsimony analyses using the heuristic search option in PAUP*. Modeltest version 3.06 (Posada & Crandall 1998) was used to select the maximum likelihood parameters, GTR+ Γ +I. The general time reversible model (Yang 1994) was used to estimate the maximum likelihood tree and branches were collapsed (creating polytomies) if the branch length was less than or equal to $1e-08$. The maximum likelihood analysis included 20 taxa. Taxa were pruned if they were part of a well-supported node (bootstrap value $>75\%$) in the parsimony tree leaving one representative of each taxon. Bootstrap values were calculated from 100 replicate likelihood analyses using the heuristic search option in PAUP*.

RESULTS

The primer combination 12St–L plus 12Sbi–H produced a single amplification product for seven species (see Table 1), but two or more bands were amplified for all other taxa. The primer pair 12SR–J–14199 plus 12SR–N–14594 was used to amplify product for sequencing for the taxa that did not produce a single amplification product using the 12St–L plus 12Sbi–H combination (see Table 1). The 12St–L primer site varied considerably in the nine taxa for which the primer pair 12SR–J–14199 plus 12SR–N–14594 was used, which may explain why the primer combination 12St–L plus 12Sbi–H did not work for all taxa. The primer 12St–L was designed as a *Tetragnatha*-specific primer (Croom et al. 1991) so it is not surprising that this site varies in lycosids. There was little variation evident in the 12Sbi–H site even though this primer was designed as specific to insects (Simon et al. 1990). The nucleotide composition was A + T-rich (44.2% A, 10.0% C, 9.8% G, 36.0% T), which is typical for arthropods (Simon et al. 1994).

Parsimony analysis yielded 2 equally parsimonious trees (Fig. 2), 482 steps long, with a consistency index, excluding uninformative

characters, of 0.415 and retention index of 0.577. Of the 330 characters included in the analysis, 172 were variable with 113 of them parsimony informative. Maximum likelihood analysis resulted in six trees with scores of 2092.1969 (Fig. 3). The six trees had the same topology because the branches were collapsed (creating polytomies) if the branch length was less than or equal to $1e-08$. The topology of the maximum likelihood trees (Fig. 3) and the parsimony trees (Fig. 2) differed mainly in the lower branches, which had less than 50% bootstrap support.

DISCUSSION

Molecular analysis confirms that most of the New Zealand or Australian lycosids included in the analysis do not belong in the Northern Hemisphere genera where they have been or are currently placed. This study confirms that *Trochosa oraria* L. Koch 1876 does not belong in the genus *Trochosa* (sensu Dondale & Redner 1990) and the two Holarctic exemplars of *Trochosa* are monophyletic, which is supported by high bootstrap values (Fig. 2). There is support for the monophyly of *Pardosa* C.L. Koch 1847 as the four exemplars form a monophyletic clade that is supported by a high bootstrap value (Fig. 3). Zehethofer & Sturmbauer (1998) also had strong support for the monophyly of the 14 exemplars of *Pardosa* that they included in their analysis. The three exemplars of *Alopecosa* Simon 1885 included in this study form a strongly supported monophyletic clade, as did the six exemplars included in the analysis of Zehethofer & Sturmbauer (1998). The exemplars of *Xerolycosa* Dahl 1908 and *Pirata* Sundevall 1833 both have good support for their monophyly. The molecular evidence suggests that *Allocosa georgicola* belongs in a *Geolycosa*-like genus, however, there is poor bootstrap support and no *Allocosa* species (sensu Dondale & Redner 1983b) were included in this analysis. *Lycosa coelestis* L. Koch 1878 does not fit the genus *Lycosa* as defined by Zyuzin & Logunov (2000) and comes out as sister to *Varacosa avara* in both analyses with reasonable bootstrap support. However, Dondale & Redner (1990) stated that *Varacosa* Chamberlin & Ivie 1942 is restricted to North America. Both trees (Figs. 2, 3) support the monophyly of the clade containing spiders with *Geolycosa*-like pedipalps

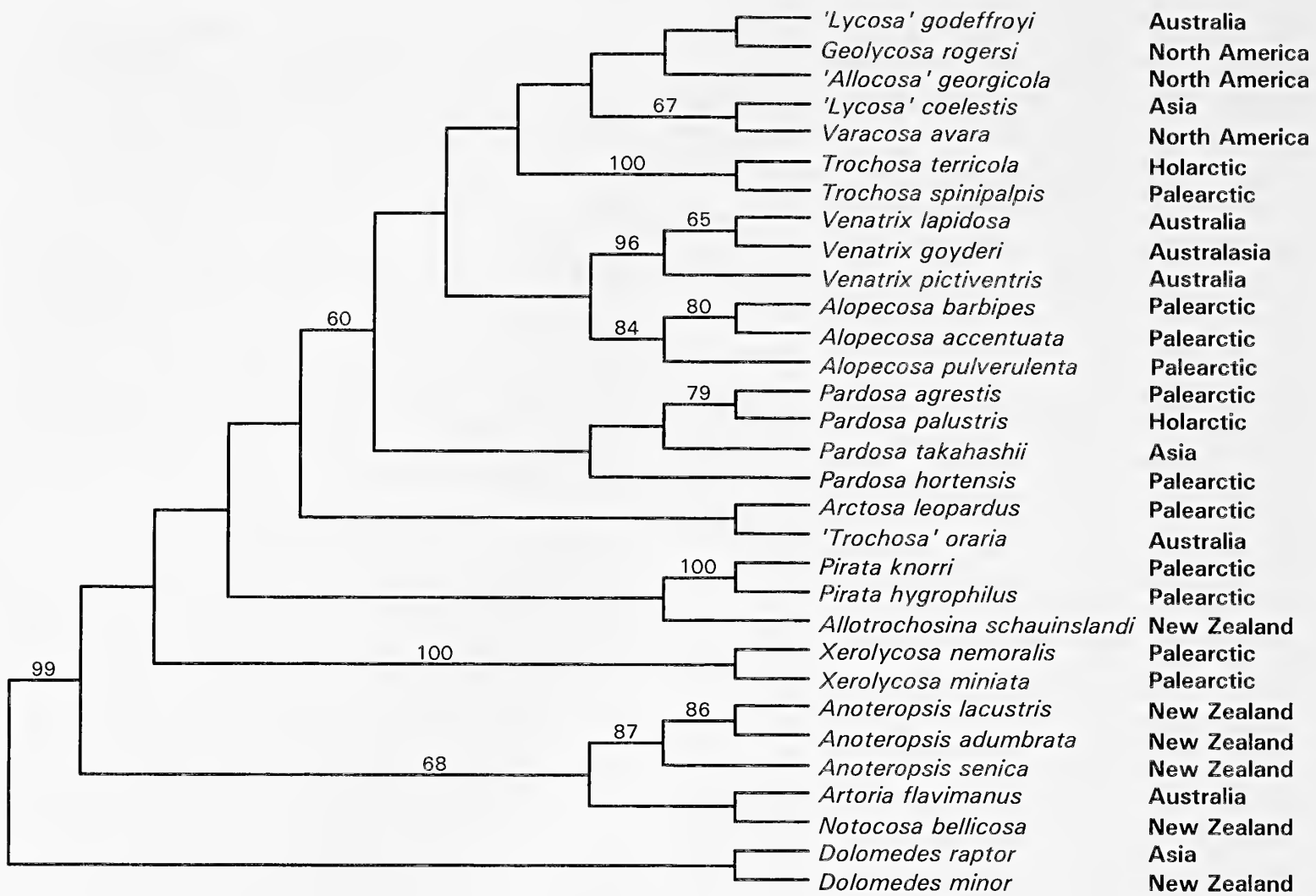


Figure 2.—One of two most parsimonious trees. The other tree differed by switching the positions of *Lycosa godeffroyi* and *Allocosa georgicola*. Bootstrap values above 50% are indicated above branches. Species distributions based on Platnick (2001) are shown on the right. Species that do not fit current generic definitions have the generic name in inverted commas.

(*L. godeffroyi*, *G. rogersi*, *A. georgicola*, *L. coelestis* and *V. avara*) but there is low (< 50%) bootstrap support for this clade. The Mediterranean genus *Lycosa* (sensu Zyuzin & Logunov 2000) is unlikely to be appropriate for *L. godeffroyi* but this cannot be inferred from our analyses because we did not sequence any Mediterranean *Lycosa* species. However, both analyses have *L. godeffroyi* coming out with *Geolycosa rogersi*, which is a true *Geolycosa*. The strongly supported, monophyletic clade of three *Venatrix* exemplars supports the monophyly of *Venatrix*. In both analyses (Figs. 2, 3) *Venatrix* was sister to *Alopecosa* and it has been noted that they share a similar pedipalpal structure (Framenau & Vink 2001). The clade containing the three *Anoteropsis* exemplars is monophyletic, which concurs with Vink (2002). *Anoteropsis* and *Notocosa* appear to be restricted to New Zealand (Vink 2002) and *Artoria* are most diverse in Australia but are also found in New Zealand, Papua New Guinea and the Philippines (Framenau 2002; Vink 2002). The

monophyly of the clade containing exemplars from *Anoteropsis*, *Artoria* and *Notocosa* is supported in both analyses and all five species share a similar pedipalp configuration (Figs. 4–8) that includes a partially divided tegulum and similarities in the position and shape of the median apophysis (Vink 2002). The relationship of *Notocosa bellicosa* (Goyen 1887) to the other four species in the clade differs between the analyses. The parsimony analysis puts *N. bellicosa* as sister to *Artoria flavimanus* Simon 1909, whereas the bootstrap support (61%) within the parsimony trees and maximum likelihood analysis have *N. bellicosa* as sister to a clade containing the other four species. This clade does not fit current subfamily definitions and, once the genera are revised, may be placed in its own subfamily.

When *Trochosa oraria* is not included in *Trochosa*, the subfamilies Pardosinae Simon 1898 and Lycosinae Simon 1898 as defined by Dondale (1986) are supported, except for *Arctosa* C.L. Koch 1847, which falls outside the Lycosinae in this analysis. Dondale (1986)

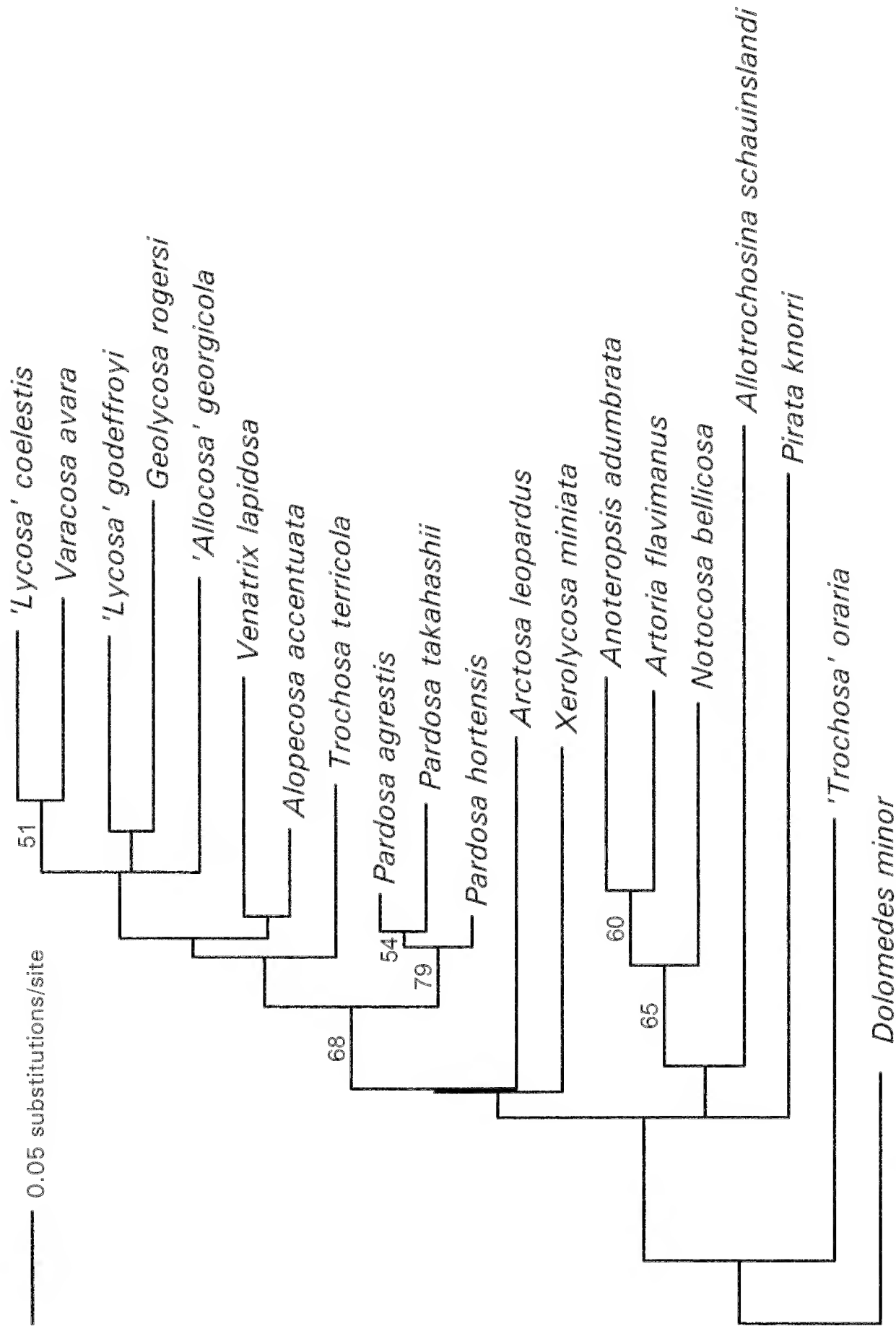
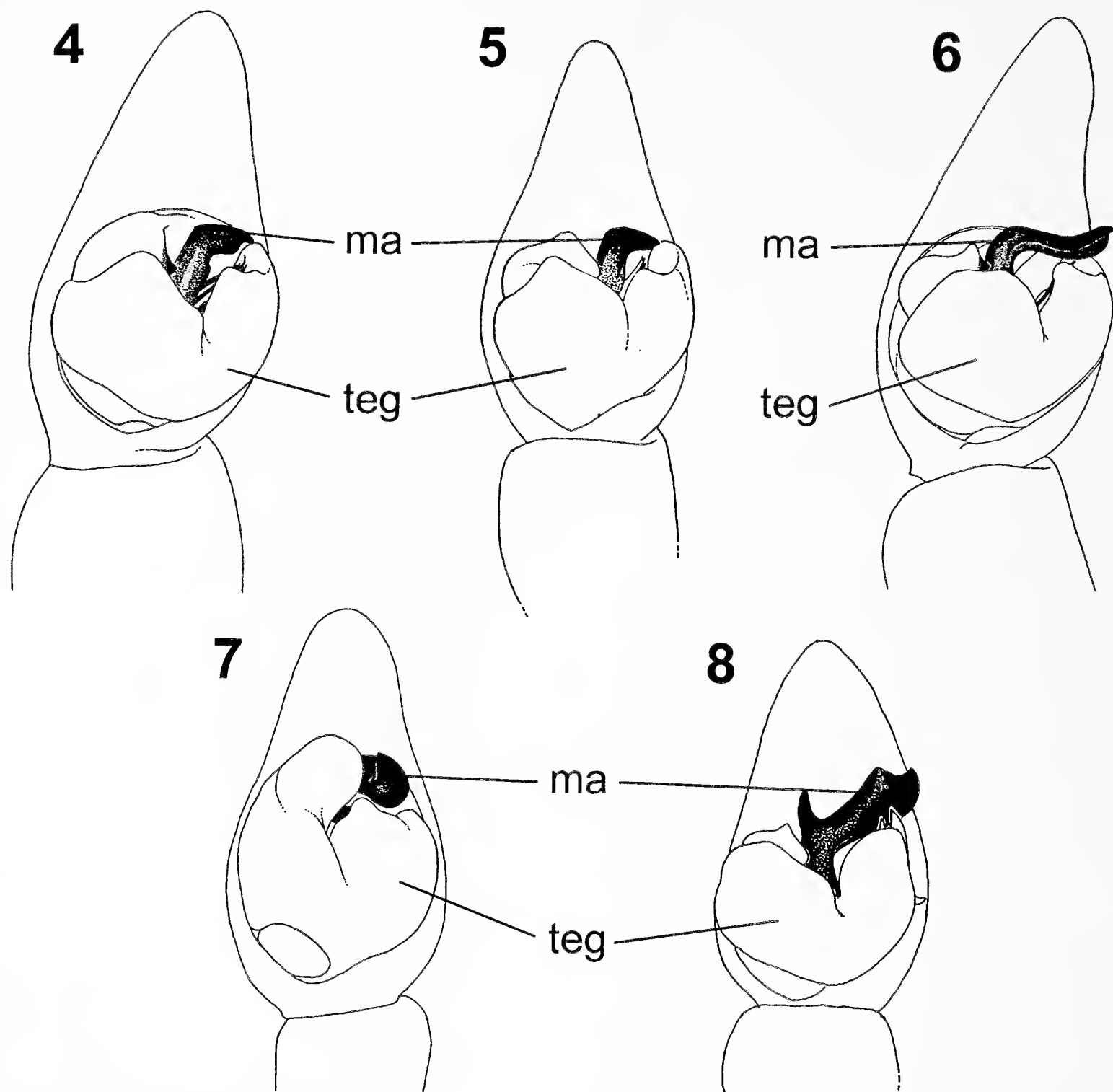


Figure 3.—Strict consensus of the six maximum likelihood trees. Bootstrap values above 50% are indicated above branches. Branch lengths are proportional to nucleotide substitutions. Species that do not fit current generic definitions have the generic name in inverted commas.



Figures 4–8.—Palps of (4) *Anoteropsis adumbrata*, (5) *Anoteropsis lacustris*, (6) *Anoteropsis senica*, (7) *Notocosa bellicosa* and (8) *Artoria flavimanus* showing partially divided tegulum (teg) and similarities in position and shape of median apophysis (ma).

suggested that the Lycosinae be divided into the “*Trochosa* group” and the “*Lycosa* group” but they are paraphyletic in our analyses. The placement of *Allotrochosina* in the subfamily Venoniinae (which also includes *Pirata* Sundevall 1833) by Vink (2001) is supported by the parsimony tree (Fig. 2) but not by the maximum likelihood tree (Fig. 3). It is worth noting that there is little bootstrap support for the lower branches of either tree. Further sequencing of several other genera may resolve these subfamily relationships.

While the pattern of distribution fits with a Gondwanan scenario a more detailed study of

genetic divergence may reveal a better approximation of the time the faunas have been separated. Preliminary analyses presented here (Figs. 2, 3) imply that Australasia had an ancestral fauna and was subsequently invaded by lycosine species, possibly via Asia through northern Australia. When New Zealand split away from Australia about 80 million years ago (Stevens et al. 1988), it is likely it retained an ancestral lycosid fauna. Only two lycosine species (*Venatrix goyderi* (Hickman 1944) and *Geolycosa tongatabuensis* (Strand 1911)) are found in New Zealand and it is likely that they have subsequently ballooned across to

New Zealand; both species are widely distributed across Australia and the South Pacific respectively but, in New Zealand, they are limited to the warmer north of the North Island.

The phylogenies presented here are somewhat preliminary, as some genera found in Australia are not represented (e.g. *Anomalosa* Roewer 1960, *Venonia* Thorell 1894, *Zoica* Simon 1898). Further resolution of subfamily relationships could also be facilitated by the inclusion of exemplars from Allocosinae Dondale 1986, Sosippinae Dondale 1986, Tricassinae Alderweireldt & Jocqué 1993, and Wadicosinae Zyuzin, 1985. The inclusion of at least one exemplar from *Lycosa* (sensu Zyuzin & Logunov 2000) may help to confirm the relationship of that genus to other lycosine genera.

Results presented here suggest that 12S DNA sequence data are useful for inferring phylogenies of closely related genera. However, these data appear to be too conservative for adequate resolution at the species level (Vink & Mitchell 2002) and too fast for deeper relationships, inferred from bootstrap support of less than 50% shown for the lower branches of the parsimony tree (Fig. 2). Deeper relationships in the Lycosidae may be better resolved by the use of an even more slowly evolving gene region, such as 28S rDNA, which has been used to infer spider phylogeny at the family level (Hausdorf 1999).

In summary, we conclude that many current generic placements of Australasian species are incorrect; the New Zealand fauna is related to a subset of the Australian fauna and parts of the Australian fauna are related to the Asian/Holarctic fauna, suggesting a subsequent invasion. Current subfamilies were found to be largely monophyletic but further work is required to fully resolve subfamily relationships.

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ARGYRODES: PHYLOGENY, SOCIALITY AND INTERSPECIFIC INTERACTIONS—A REPORT ON THE ARGYRODES SYMPOSIUM, BADPLAAS 2001

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ABSTRACT. *Argyroides* Simon 1864 is a large, cosmopolitan theridiid genus whose members exhibit a wide range of foraging techniques which usually involve exploiting other spiders, either by using their webs, stealing their food, or preying on them directly. We held a symposium on this genus at the 15th International Congress of Arachnology, Badplaas, South Africa in order to obtain a clearer perspective on the relationship between the phylogeny of the genus and the different foraging techniques. We concluded that *Argyroides* forms a monophyletic group within the Theridiidae, and that there are clear monophyletic clades within the genus (already identified as species groups) that appear to share behavioral characteristics. We found no clear indication that foraging behaviors such as kleptoparasitism (stealing food) evolved from araneophagy (eating spiders) or vice versa. However, it appears that species that specialize in either kleptoparasitism or araneophagy use additional techniques in comparison to species that readily use both foraging modes. During our examination of *Argyroides*/host interactions we noted the importance of *Nephila* species as hosts of *Argyroides* species around the world and the impact of *Argyroides* on *Nephila*. We also noted the fluid nature of the relationship between *Argyroides* and the spiders with which they interact. For example, an *Argyroides*/host relationship can change to an *Argyroides*/prey relationship, and the type of kleptoparasitic behavior employed by an *Argyroides* can change when it changes host species. The importance of eating silk was also noted and identified as an area for further research. We concluded that more work involving international collaboration is needed to fully understand the phylogeny of the genus and the relationships between the different types of foraging behaviors.

The large (over 200 species) cosmopolitan spider genus *Argyroides* has attracted interest worldwide because of the gregarious nature of

many of its species and their unusual foraging techniques (which include invading webs to steal food from and to attack other spiders). In response to increasing international attention in this group we decided to hold a symposium on *Argyroides* to consolidate our knowledge and obtain an overall perspective on the genus. Our

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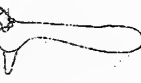
Species groups	Male cephalo-thorax	Recognized feeding methods					
		Glean insects	Steal foodbundles	Feed with host	Attack moulting host	Catch spiders by lunging	Catch spiders with a net
							
<i>argyroides</i>		✓	✓	✓	✓	✓	X
<i>cancellatus</i>		✓	✓/X	✓/X	?	?	?
<i>cordillera</i>		?	?	?	?	?	?
<i>trigonum</i>		✓	✓	?	✓	✓	X
<i>rhomphaea</i>		?	X	X	?	X	✓
<i>ariamnes</i>		?	X	X	?	X	✓

Figure 1.—Chart of the six recognized species groups of *Argyroides* (from the Americas) indicating the current known foraging behaviors and the standard form of the male cephalothorax for each group. A tick indicates that a species from that group performs the foraging technique, a cross indicates that a species is known not to perform this behavior, and a question mark indicates that nothing is known about the foraging method in relation to the species group. A tick and a cross for the same foraging method indicates that some species in this group use the foraging method while other species do not.

aim was to identify the direction that the research was leading, and develop future research programs that are more integrated.

The symposium was loosely focused on understanding how the phylogenetic relationships within the genus reflected the evolution of different types of relationships with other spider species. The “interaraneae” relationships of *Argyroides* species are very diverse. Some species behave as kleptoparasites in that they invade the web of a (usually larger) host spider and eat the host’s web, glean insects off the host’s web, steal the host’s wrapped food bundles, and/or feed with the host. Some species attack the host when it is vulnerable such as during molting, or capture and eat small spiders by lunging at them and grabbing them with their front legs. Still others capture spiders by throwing a line of sticky silk over the victim. Phylogeny provided a framework in which we discussed 1) these diverse interspecific interactions, 2) sociality, and 3) specific

foraging techniques. Below is a report on the conclusions we drew from the symposium and the areas that still require more research.

Evolution.—Evolutionary relationships within the genus *Argyroides* are poorly understood. Currently there are six recognized species groups (Exline & Levi 1962) within the genus: *Argyroides*, *Rhomphaea*, *Ariamnes*, *Cordillera*, *Cancellatus*, and *Trigonum*. Because these names refer to species groups and currently not to genera, they are not in italics. It is confusing that “*Argyroides*” refers to the whole genus and to a particular species group. In this text, when we refer to the genus *Argyroides* we will use italics, but when we refer to the species group *Argyroides*, we will use normal script. The evidence to date suggests that animals in the species groups may use similar methods of web invasion (Fig. 1). For example, all species so far studied in the *Rhomphaea* and *Ariamnes* species groups seem to specialize on araneophagy (Eberhard

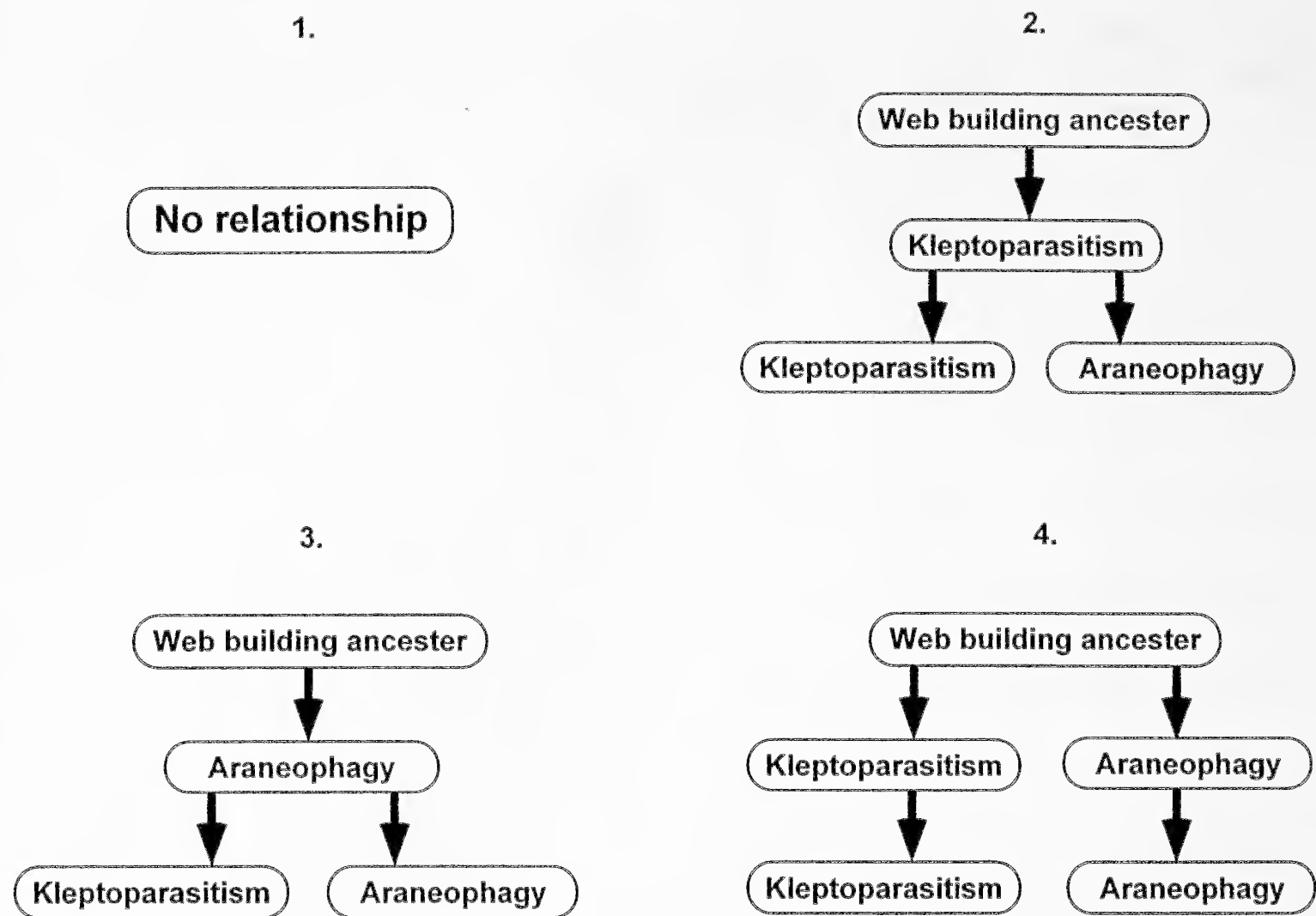


Figure 2.—Four ways in which the evolution of araneophagy and kleptoparasitism may be related. See text for details of each model.

1979; Horton 1982; Whitehouse 1987). They tend to be free-living and solitary, and capture spiders by throwing a sticky silk line over the victim. Species from the *Argyrodes* species group are gregarious and seem to specialize on kleptoparasitism. They will even feed with the host to obtain food: *A. antipodanus* O.P. Cambridge 1880 (Whitehouse 1986, 1997; Grostal & Walter 1997); *A. elevatus* Taczanowski 1872 (Vollrath 1979, 1984); *A. argentatus* O.P. Cambridge 1880 (Robinson & Robinson 1973); *A. argyrodes* 1842 (Kullmann 1959). Species that have been studied from the *Trigonum* species group forage using both kleptoparasitism and araneophagy: *A. trigonum* Hentz 1850 (Cangialosi 1997; Larcher & Wise 1985; Suter, et al 1989) and *A. baboquivari* Exline & Levi 1962 (Larcher & Wise 1985). However, the araneophagy that *A. trigonum* (at least) uses is distinct from that of *Rhomphaea* and *Ariamnes* species. Cangialosi reported in the symposium that it does not throw silk in order to capture the spider, but kills the spider by biting it. The species group *Cancellatus* contains some members that will

only glean insects and eat the host's silk (*A. caudatus* Taczanowski 1874: Henaut & Ibarra-Nunez unpubl. data; Vollrath 1984) and other members that will also feed with the host (*A. globosus* Keyserling 1884: Henaut 2000) and others which will not feed with the host, but will steal food bundles (*A. ululans* O.P. Cambridge 1880: Cangialosi 1990a, b). Thus in the *Cancellatus* species group there is no consistency in the kleptoparasitic techniques used. No spiders from the *Cordillera* species group have been studied.

Four pathways have been proposed by which kleptoparasitism and free-living araneophagy may have evolved (Fig. 2). First, ecological pressures, rather than evolutionary history, may have dictated which behavior is expressed in each species so that there is no phylogenetic relationship between phylogeny and behavior (Model 1). Alternatively, araneophagy and kleptoparasitism may each have evolved once, in which case there are three possible models: Free-living araneophagy may have evolved from kleptoparasitism (Model 2). Smith Trail (1980) argued that the

kleptoparasitic skills of interpreting the host's vibrations could preadapt *Argyrodes* for safely stalking and capturing the host itself. Alternatively, kleptoparasitism may have evolved from araneophagy (Model 3). Vollrath (1984) supported this model although he argued that *Argyrodes* would initially invade other spiders' webs and chase out the owner, and then later adopt araneophagic behaviors that would preadapt them to kleptoparasitism. Finally, both kleptoparasitism and araneophagy may have evolved separately (Model 4). Whitehouse (1987) proposed this argument based on differences in the araneophagic techniques of species from the predominantly araneophagic (*Rhomphaea* and *Ariamnes*) and kleptoparasitic (*Argyrodes*) species groups.

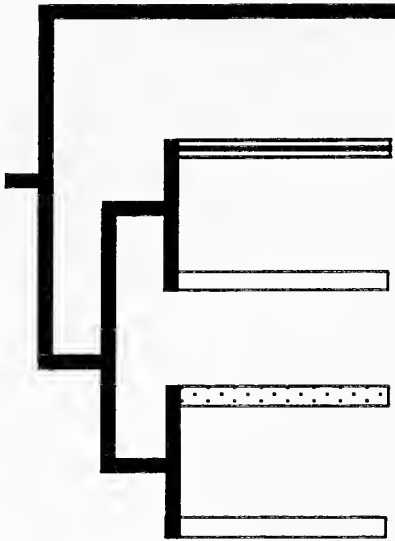
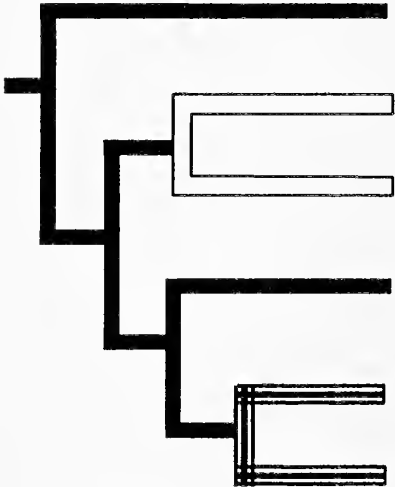
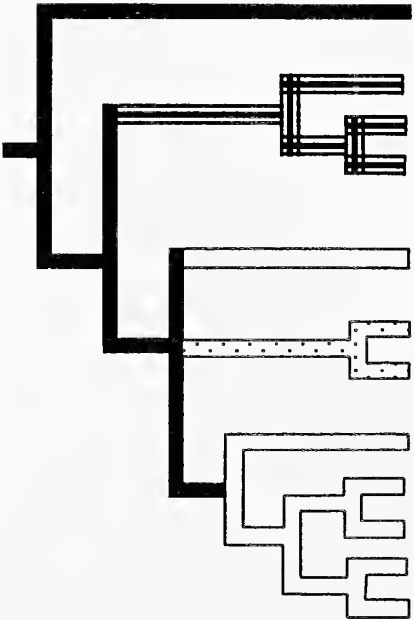
The three phylogenetic studies presented at this symposium examined the relationship between these different species groups and their foraging techniques, in particular the relationship between species that are predominantly kleptoparasitic, and those that are predominantly araneophagic (Fig. 3). Agnarsson presented a phylogenetic tree of *Argyrodes* (largely from the Americas) within the context of the family Theridiidae, and used sequences from the genes CO1, 16S, 18S and 28S and morphological characters to construct the tree. Masumoto, working on Japanese species, constructed his tree using sequences from the gene CO1, while Whitehouse presented trees of Australian *Argyrodes* based on sequences from the genes CO1 and 16S (for more information see Agnarsson et al. this journal, Masumoto unpubl. data, Whitehouse et al. unpubl. data).

Superficially, all three trees appear to support different models: Agnarsson's tree seems to support model 1 (no evolutionary relationship between developing araneophagy and kleptoparasitism); Masumoto's tree seems to support model 2 (araneophagy developed from kleptoparasitism) and Whitehouse's tree seems to support model 3 (kleptoparasitism developed from araneophagy). However Bremer support for the lower nodes are not strong in any tree, and relationships between species could easily switch around. In addition the trees suggest that the basal species within the genus *Argyrodes* use both kleptoparasitic and araneophagic behaviors, even though they lack the more derived techniques of these foraging methods (such as the more derived kleptoparasitic behavior of "feeding with the host", or the ara-

neophagic behavior of "throwing a sticky thread over the prey"). The behavior of the basal species of both Agnarsson's and Masumoto's trees directly fit this model, while the behavior of the basal species in Whitehouse's tree is not known, except that it occurs on a larger spider's web. Consequently, the available evidence to date suggests that the araneophagic and kleptoparasitic foraging behaviors of *Argyrodes* species evolved concurrently, and latter species may have specialized, and/or refined these techniques.

In addition, all three trees support some general claims. For example, the trees of both Agnarsson and Whitehouse indicate that *Argyrodes* and *Ariamnes* are sister species groups, while all three trees suggest that the *Rhomphaea* species group is quite distinctive. This suggests that *Rhomphaea* and *Ariamnes* may have developed araneophagic foraging techniques independently of each other.

It is intriguing that *Rhomphaea* and *Ariamnes* may have developed araneophagy independently because the technique they both use to capture spiders (throwing silk) is distinctive from the technique used by the basal *Argyrodes* species (biting/lunging). At the symposium we debated whether the spider-catching behavior of *Ariamnes* and *Rhomphaea* was plesiomorphic or derived. Most symposium members (who have not seen *Ariamnes* or *Rhomphaea* catch spiders) regarded it as a plesiomorphic theridiid trait because most theridiids catch prey by wrapping them with sticky silk. Whitehouse argued that the behavior is derived because it is very distinctive from normal theridiid wrapping. Theridiids normally attack prey by throwing numerous threads of silk in quick succession with alternating legs IV over the victim until it is completely covered. When *Rhomphaea* and *Ariamnes* attack prey, the two legs IV move in unison towards the prey, and the spider will throw one to five sticky threads. Once the prey is immobilized *Rhomphaea*/*Ariamnes* will assume normal theridiid wrapping behavior. Whitehouse conceded that within these two species groups there might be a continuum in that some species may throw silk more like a standard theridiid while others may be more distinctive and more stylized. Agnarsson suggested that a solution would be to look for the spigots on the spinnerets that are responsible for producing sticky silk in theridiids. He noted that individuals in the *Argy-*

	Species group	Behaviors
Agnarsson 	Trigonum	Kleptoparasitic & Araneophagic (bite/lunge)
	Rhomphaea	Araneophagic (line throwing)
	Cancellatus	Kleptoparasitic
	Ariamnes	Araneophagic (line throwing)
	Argyrodes	Kleptoparasitic
Masumoto 	Unknown	Kleptoparasitic & Araneophagic (bite/lunge)
	"Argyrodes"	Kleptoparasitic
	Unknown	Kleptoparasitic??
	"Rhomphaea"	Araneophagic (line throwing)
Whitehouse 	Unknown	Kleptoparasitic??
	"Rhomphaea"	Araneophagic (line throwing)
	"Argyrodes"	Kleptoparasitic
	"Ariamnes"	Araneophagic (line throwing)
	"Argyrodes"	Kleptoparasitic

rodes (“kleptoparasitic”) species group have lost one of the two aggregates on each PLS. Miyashita added that kleptoparasitic *Argyrodes* also lack an aggregate gland for producing sticky silk. If basal species do not have these spigots and an aggregate gland, then this would suggest that spider-catching method used by *Rhomphaea* and *Ariamnes* species is derived. If basal species do have these structures, then “throwing silk” is more likely to be a plesiomorphic trait.

Our discussions on the phylogeny of *Argyrodes* emphasized the need for more information. Firstly we need a more comprehensive phylogenetic tree to identify all species groups. We concluded that currently named species groups (*Argyrodes*, *Rhomphaea*, *Ariamnes* and *Trigonum*) appear to be monophyletic and therefore useful groupings of the species. However these species groups are only specific for American species, and that species in other continents, like Asia, Australia and Africa, may form different species groups. We concluded that we need an integrated, comprehensive phylogenetic tree that includes species found throughout the world, to establish if species groups within the *Argyrodes* complex are indeed monophyletic and should be recognized as separate genera.

Secondly, we acknowledged that there is a huge lack of behavioral data, and that it is unlikely that we can obtain behavioral data from each of the 200 species worldwide. We concluded that a better approach would be to identify the monophyletic species groups within the genus and then focus on particular species within these groups. Henaut expressed caution with this approach. His point was well taken as the large *Cancellatus* species group is known to contain a species (*A. globosus* Henaut 2000) that can do a range of kleptoparasitic techniques including feeding with the host, while it also contains a species (*A. caudatus*) which has been studied intensively (Vollrath 1984, Henaut & Ibarra-Nunez unpubl. data) but which only gleans insects from around the edge

of webs. Because of the size of the group and the morphological diversity within the group it is possible that *Cancellatus* is not monophyletic. A comprehensive phylogeny would reveal this. Nevertheless we need to show caution when deciding which species will be representative of species groups.

Sociality.—An interesting aspect of the theridiid phylogeny that Agnarsson pointed out and which he discusses in this volume (Agnarsson et al 2001) was that *Argyrodes* form a monophyletic clade with the genera that contain social spiders. One of the striking characteristics of many species of *Argyrodes* is that they are gregarious, even forming mixed species groups around other spider’s webs. Their location within the theridiid phylogeny suggests that they may have a phylogenetic predisposition to form groups.

The significance of the group-forming behavior may be that it enhances the effectiveness of kleptoparasitism. For example, many *Argyrodes* on the same host’s web will be producing vibratory signals from numerous directions, confusing the host. Henaut pointed out that distraction had the effect of cooperation. He observed *A. globosus* distract the host while another *A. globosus* stole the food. He also saw *A. globosus* vary its degree of gregariousness—it was more gregarious on the webs of the more aggressive host (*Leucauge mariana* Taczanowski 1881, *L. venusta* Walckenaer 1842 and *L. argyra* Walckenaer 1842) than the less aggressive host (*Gasterancantha cancriformis* (Linnaeus 1758)).

Host-*Argyrodes* interactions.—Another important theme in the symposium was the relationship between hosts and *Argyrodes*. Firstly, Miyashita looked at the effect of different types of host species on the distribution of *Argyrodes* in Japan. He found that *Argyrodes* were limited by the distribution of their hosts and that *Nephila* spp. were particularly important. Li also pointed out the strong relationship between *Argyrodes* and *Nephila* in Singapore, and this relationship has also been noted in the Americas

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Figure 3.—Phylogenetic trees of species groups within *Argyrodes* reported by Agnarsson, Masumoto and Whitehouse at the symposium, indicating foraging behaviors associated with the species groups. Only spiders from the Americas (Agnarsson’s tree) have been formally assigned to the different species groups, so the speech-marks indicate the most probable species groups for the spiders from Japan (Masumoto) and Australia (Whitehouse).

(Vollrath 1979) and in Australia (Elgar 1989, 1993; Grostal & Walter 1997). As Smith noted, the importance of *Nephila* spp. as a host species for *Argyrodes* appears to be pandemic.

Secondly, the actual relationship between host and *Argyrodes* was explored. Li and Cangialosi emphasized that species of *Argyrodes* are often assumed to be kleptoparasitic (i.e. derogatory to the welfare of the host) when they could be commensal (have no effect on the host). Li provided evidence that *A. flavescens* O. P. Cambridge 1880 did have a direct affect on its host *Nephila pilipes* (Fabricius 1793). In the presence of the kleptoparasite, *N. pilipes* were smaller and produced fewer, but larger eggs. We concluded that the effect of *Argyrodes* on the fitness of the host was an area that could be expanded.

Thirdly, the relationship between the host and the *Argyrodes* can change depending on the type of host, and even the developmental stage of the *Argyrodes*. Cangialosi, working with a phylogenetically basal species *A. trigonum*, demonstrated that while this species exhibits both araneophagy and kleptoparasitism for all three hosts that she has studied; it is predominately a predator of *Nerienne radiata* (Walckenaer 1842) (Linyphiidae) and predominately a kleptoparasite of *Pityohyphantes costatus* (Hentz 1850) (Linyphiidae) and *Achaearanea tepidariorum* (C. L. Koch 1841) (Theridiidae).

Whether *A. trigonum* behaves as a kleptoparasite has to do not only with relative host size, but also with the developmental stage of *Argyrodes* independent of its relative size. For example, older *A. trigonum* are more likely to be aggressive compared to juveniles, regardless of host size.

Although *A. trigonum* switched between kleptoparasitism and araneophagy, the behavioral repertoire within each of these categories was limited. Kleptoparasitically, Cangialosi reported that *A. trigonum* gleaned insects and stole prey, but that it did not feed with its host (a kleptoparasitic behavior common in the *Argyrodes* species group) or eat silk. Araneophagically, Cangialosi reported that *A. trigonum* attacked spiders by biting them, but that it did not throw a silk line over a prey spider in order to catch it (the araneophagic method of species in the Rhomphaea and Ariamnes species groups).

Nevertheless the change in the relationship

between *A. trigonum* and its host (from kleptoparasite/host to predator/prey) provides another dimension to the "interaraneae" interactions within the genus *Argyrodes*. The flexibility of the ability to change and the ecological ramifications of the change for both the host and the kleptoparasite were discussed and seen as important areas for future development.

Many questions remain concerning the factors contributing to changes in the relationship between *Argyrodes* species and their hosts. Basal species, such as those from the *Trigonum* species group which exhibit a wide repertoire of foraging behaviors, not only provide insight into the evolution of kleptoparasitism and araneophagy, but (as both Miyashita and Cangialosi pointed out) can also be good models for studying how shifting behavioral relationships between species can translate into complex patterns of population dynamics.

More subtle changes in the relationship between *Argyrodes* and their hosts were also presented at the symposium. Henaut showed that *A. globosus* would only use the behavior "feeding with the host" with the less aggressive hosts (*Gasterancantha cancriformis*, *Verucosa arenata* (Walckenaer 1842), and *Nephila clavipes* (Linnaeus 1767)) and would form larger groups around the webs of the more aggressive host (*Leucauge mariana*, *L. venusta* and *L. argyra*) that had the effect of distracting the host.

An unusual relationship highlighted by Smith was that between an unnamed species of *Argyrodes* and plants protected by ants (Fowler & Venticinque 1996). In this case *Argyrodes* is not interacting with other spider species but with ants. How the *Argyrodes* interacts with the ants, and how this species of *Argyrodes* relates phylogenetically to other *Argyrodes* species, are two additional areas of research that need developing.

Silk eating.—Both Miyashita and Smith emphasized the importance of *Argyrodes* consuming the silk of its host. Miyashita pointed out that this behavior enables *Argyrodes* to survive periods of low prey abundance in the host's web. It would be interesting to know how widespread this behavior is (Cangialosi reported that she has not seen *A. trigonum* feed on silk despite many hours of observations). Many species of spiders eat their own silk; do many species eat other spider's silk as well? This area also needs further investigation.

Conclusions.—Research within the genus *Argyroides* is at a very interesting stage. Our first priority is to improve our understanding of the phylogeny and its relationship to the multitude of foraging techniques common within the genus. With these points clarified we can more easily address ecological questions concerning interspecific interactions between *Argyroides* and their “hosts”. Our results suggest that different ecological questions may be particularly relevant for different species groups. For example, members of the *Trigonum* species group may be particularly useful for investigating a switch from kleptoparasitic behaviors to predatory behaviors. Species in the *Argyroides* species group may be useful when asking questions either about host specificity or conditions under which an *Argyroides* should change its kleptoparasitic techniques.

Obviously, these topics are only the tip of the iceberg. Our symposium only touched on the question of *Argyroides* and sociality, the role of crypsis in determining the striking morphology of many *Argyroides* species, and how *Argyroides* locate their hosts. Mixed species groups of *Argyroides* were not discussed, and we did not mention courtship behavior at all. All this indicates a very exciting and interesting future for behavioral-ecology research within the genus *Argyroides*.

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ULTRAVIOLET REFLECTANCE OF SPIDERS AND THEIR WEBS

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ABSTRACT. To determine the reflectance of spider webs and spiders under ultraviolet (UV) light, spiders and their webs were photographed under normal (white) light and under UV light. It was found that all silk in araneoid webs reflect slightly more UV light than white light; i.e., they had a positive UV-brightness. However, the often cited, particularly high UV-brightness of stabilimenta could not be confirmed. Spiders differed in their UV-brightness, with most spiders reflecting less UV light than white light. Based on the knowledge of the visual system of insects and invertebrates it is suggested that the main function of stabilimenta is predator defense. However, drawing a final conclusion requires more knowledge on the way potential predators and prey perceive spiders, spider webs and stabilimenta.

Keywords: Stabilimentum, camouflage, predator-prey, spider silk, visibility

The function of stabilimenta in orb-webs is the subject of an intense debate. Originally, it was suggested that stabilimenta serve to stabilize the web, hence the name stabilimentum (Simon 1893). More recent studies suggest that in most species, stabilimenta serve a visual function towards prey and/or predators of the spiders, also reflected in the fact that no spider species that removes the web during the day is known to build a stabilimentum (Herberstein et al. 2000). However, whether prey or predators are the intended viewers of stabilimenta remains hotly debated. Results of several studies that showed that stabilimenta attract prey could not be confirmed by others. The function of stabilimenta to deter or confuse predators is equally disputed, especially since it is not easily amenable to experiments (for a review see Herberstein et al. 2000). Predatory spiders that have recently been shown to use stabilimenta to find their prey spider (Seah & Li 2001) are quite certainly not the intended viewers of the stabilimenta.

Craig & Bernard (1990) assessed the reflectance of spider silk by measuring the reflectance of individual silk strands for wavelengths between 340 and 700 nm at 10 nm increments. They concluded that cribellate sticky silk and stabilimenta, but not other silk types of araneoid orb-webs, have a high reflectance in the ultraviolet (UV) spectrum. In a later study using the same method, Craig et

al. (1994) argue that silk of primitive spiders and cribellate silk of uloborids have a high UV reflectance whereas derived (araneoid) aerial web spinners produce viscid silks that are spectrally flat or have a low UV reflectance. Watanabe (1999) measured the reflectance of the stabilimentum of a uloborid species and found that it was fairly flat, with a slightly higher reflectance in the UV range. The high UV reflectance of stabilimenta has been considered by several authors to be an attractor for prey (Craig & Bernard 1990; Tso 1998; Watanabe 1999), whereas other authors have questioned this function (Eisner & Nowicki 1983; Blackledge 1998b; Blackledge & Wenzel 1999, 2000).

Most, if not all, spiders that build a stabilimentum sit on the hub of the web (Scharff & Coddington 1997). However, the appearance under UV light of the web together with the spider has been documented only once with three pairs of photographs of a single species taken in the field (Craig & Bernard 1990). Taking comparative pictures in the field is problematic since lighting is neither constant nor controllable. The aim of the present study is to compare the appearance of spiders and their webs under UV light and white light under standardized lighting conditions. In particular I asked the following questions: 1. can the results of Craig & Bernard (1990) and Craig et al. (1994) be confirmed using an

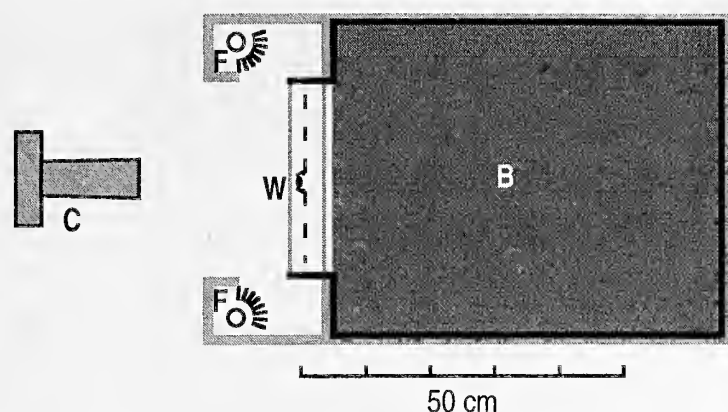


Figure 1.—Layout of the 'black box' (modified after Langer & Eberhard 1969) used to take the pictures, seen from above. B = box lined with black velvet, C = camera, F = fluorescent bulbs (vertical) and W = web with the spider. The bulbs used were either UV bulbs for the UV treatment or white bulbs for the white light treatment (cf. Fig. 2).

alternative technique and 2. what is the appearance of web building spiders under UV light.

METHODS

Spiders were collected in the wild and acclimatized to laboratory conditions where they built webs in acrylic plastic frames (30 x 30 x 5 cm). The frames with the spiders were placed at the front of a 'black box' (Fig. 1) and photographed there. Each spider in its web was photographed under UV light and under white light (Fig. 2). Unless indicated otherwise, whenever 'white' is used in the present paper, it implies white to the human eye. Light was switched between UV and white by exchanging the fluorescent bulbs, thus ensuring that, apart from the spectral distribution, lighting was identical in both treatments. Pictures were taken with a Nikon F camera with a 105 mm UV lens and, where necessary, a Nikon M2 macro adapter on Kodak Tri-X Pan 400 ASA B/W film (this film has a high sensitivity down to 300nm; Kodak, pers. comm). For pictures taken under UV light, a UV transmitting 'black' filter was placed in front of the lens. Pictures under UV light were exposed for 3 sec and those under white light for 1 sec. These exposure times resulted in the same shade of gray when taking a picture of a standardized Kodak gray card, which reflects 18% of the incident light across all wavelengths. The gray card was photographed together with the spider at the edge of all pictures (visible at lower edge of Figs. 9, 10, 13, 14). For all spider pictures, an

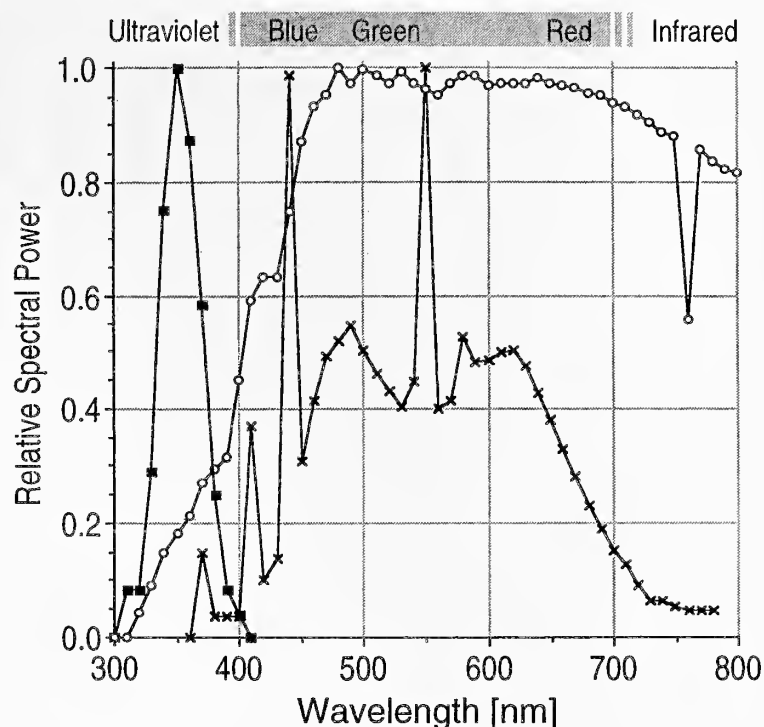


Figure 2.—Relative spectral irradiances of sunlight (open circles), and of the artificial lights used (black squares: UV fluorescent bulbs Sylvania black light 'F15W/BLB -T8', crosses: Osram 'L 15W/12-950—Daylight'). Curves were normalized to have their maximum at 1.0. The gray bar at the top indicates the range of wavelengths visible to humans.

aperture of $f = 16$ was used. Negatives were developed commercially, which resulted in slight differences in development between films. However, both pictures of one object were always on the same film and therefore underwent identical development.

Negatives were scanned with a Polaroid 'SprintScan35' slide scanner. After scanning, contrast was enhanced by 20 steps with Adobe Photoshop. To allow exact comparison, brightness and contrast of the picture were further adjusted in such a way that the brightness value of the gray card and the brightness value of the dark background were the same in both pictures of each pair.

The reflectance of spider, silk and stabilimenta was estimated by measuring their brightness value (in percent, ranging from 0 = black to 100 = white) at the same position in the two pictures using the utility Apple DigitalColour Meter on pictures that were suitably enlarged or reduced with Photoshop. For the measurements of the brightness values of the different kinds of silk, four pairs of measurements were taken for each picture and silk type. The brightness of each spider was measured three times, once on the cephalothorax and twice on the abdomen. A measurement of the absolute brightness of the silk or

Table 1.—Reflectance of spiders under UV light and under white light. Values for debris and egg sac stabilimenta are given in the text. Abbreviations: CH = Switzerland; KE = Kenya, LK = Sri Lanka; MX = Mexico; SG = Singapore; ZA = South Africa.

Species	Origin	UV-brightness			
		spider	dry silk	sticky silk	silk stabilimentum
<i>Achaeraranea lunata</i> (Clerck, 1757)	CH	−15	15		
<i>Agelenatea redii</i> (Scopoli, 1763)	CH	−2	12	10	11
<i>Arachnura</i> sp.	LK	−14	12		
<i>Araneus diadematus</i> Clerck, 1757	CH	−14	14	11	
<i>Araneus quadratus</i> Clerck, 1757	CH	−8	10	2	
<i>Argiope argentata</i> (Fabricius, 1775)	MX	−2	8	6	6
<i>Argiope bruennichi</i> (Scopoli, 1772)	CH	−5	6	3	8
<i>Argiope versicolor</i> (Doleschall, 1859)	SG	−18	7	8	
<i>Cyclosa conica</i> (Pallas, 1772)	CH	−1	6	12	9
<i>Cyclosa insulana</i> (Costa, 1834)	ZA	−3	14	12	8
<i>Cyclosa turbinata</i> (Walckenaer, 1842)	MX		15	11	
<i>Cyclosa walckenaeri</i> (O.P.-Cambridge, 1889)	MX	−11	9	12	11
<i>Cyrtophora citricola</i> (Forskål, 1775)	ZA	−5	8		
<i>Micranthema gracilis</i> (Walckenaer, 1805)	MX	−14	12		
<i>Nephila senegalensis</i> (Walckenaer, 1842)	KE	−2	5	−1	
<i>Nephila</i> sp.	ZA	−2	23	15	
<i>Steatoda triangulosa</i> (Walckenaer, 1802)	CH	−18	7		
<i>Uloborus</i> sp.	ZA	−23	16	25	11
<i>Verrucosa arenata</i> (Walckenaer, 1842)	MX	2	7	9	
<i>Zilla diodia</i> (Walckenaer, 1802)	CH	−1	16	15	
<i>Zosis geniculatus</i> (Olivier, 1789)	LK	4	18	26	16

the spider in comparison with the gray card was not possible because the brightness of the silk largely depends on its position relative to the light source (cf. brightness of radii within Figs. 11, 12) and because the position of the gray card differed from one pair of pictures to the next.

The relative reflectance of the silk and the spiders was then assessed by subtracting the brightness value under white light from the brightness value under UV light. I will use the term UV-brightness for this difference. Positive UV-brightness values indicate higher brightness under UV than under white light. Nomenclature of orb-web elements follows Zschokke (1999).

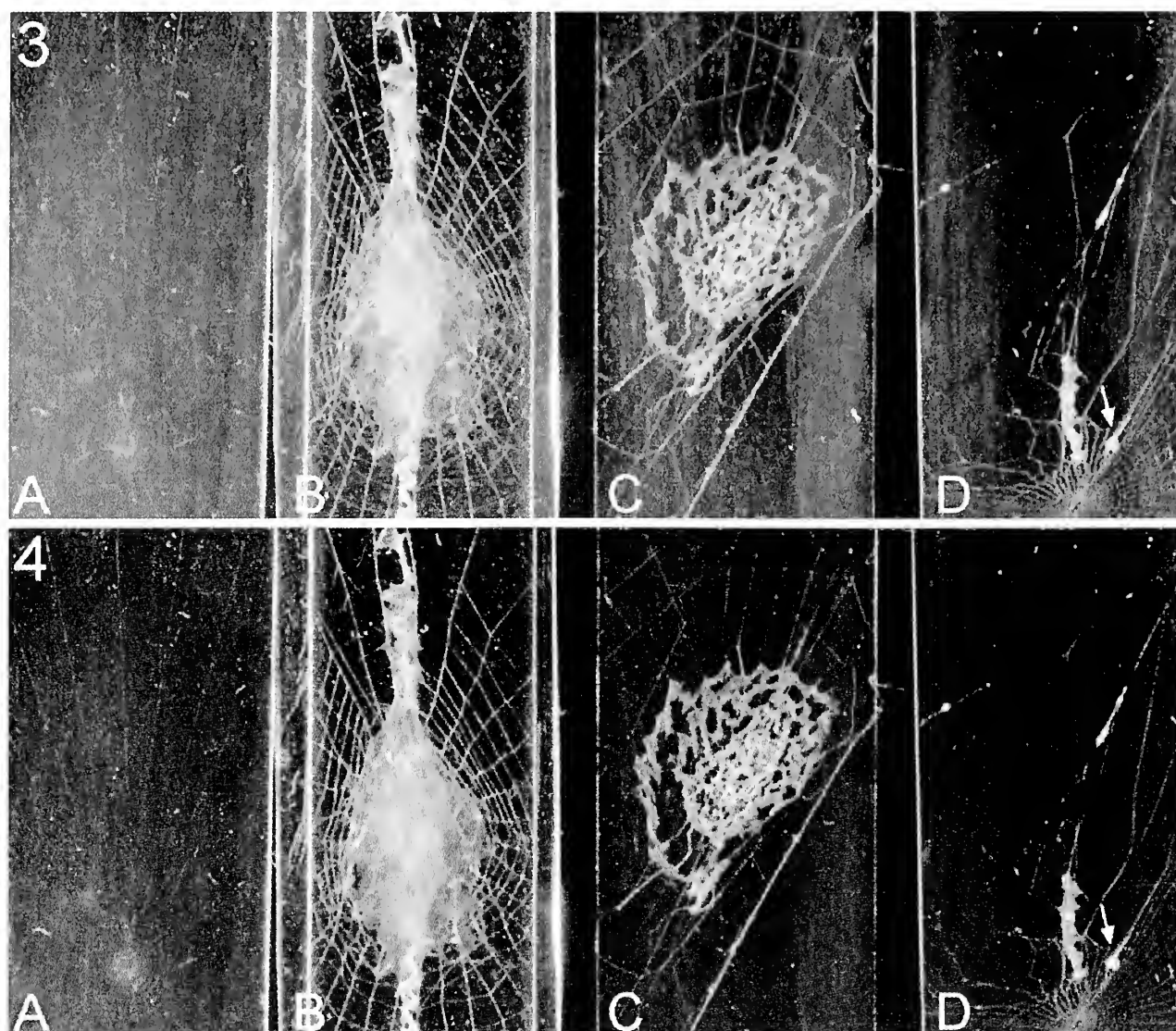
RESULTS

Reflectance of silk.—I found that all silks (dry silk, cribellate and ecribellate sticky silks, stabilimenta) reflected UV light better than white light, i.e., had a positive UV-brightness (Table 1; Figs. 3, 4).

Most kinds of silk had an intermediate, pos-

itive UV-brightness (ecribellate sticky silk: + 9, araneid and nephiline dry silk: +11; theridiid dry silk: +11; uloborid stabilimentum: +13; araneid silk stabilimentum: +9), cribellate sticky silk had the highest UV-brightness (+25), dry silk of uloborid webs also had a high UV-brightness (+17), whereas detritus stabilimenta (wrapped prey remains and shed skins) of *Cyclosa conica* and *C. insulana* both showed a neutral UV-brightness (+1 & 0), and the egg sac ‘stabilimentum’ (Levi 1977) of *C. turbinata* even had a negative UV-brightness (−6). Similarly, the cocoon of *A. versicolor* was also found to have a negative UV-brightness (−9).

Reflectance of spider.—Most spiders appeared darker under UV light than under white light, i.e., had a negative UV-brightness. However, there was some variation between species, ranging from fairly low UV-brightness to neutral UV-brightness (Figs. 5–12, Table 1). Only a few of the species analyzed showed different patterns under UV light compared to white light: the bright yellow ab-



Figures 3–4.—Stabilimenta and hub decorations of *Zilla diodia* (A), *Argiope bruennichi* (B), *Zosis geniculatus* (C) and *Cyclosa conica* (D) mounted on microscope slides photographed under UV light (3) and white light (4). The stabilimentum of *C. conica* is a pure silk stabilimentum. The small bright spot to the right of the stabilimentum (arrow) is the wrapped remains of a fruit fly *Drosophila* sp., as it is sometimes incorporated into the stabilimentum.

dominal spots of *Nephila senegalensis* disappeared under UV light (Figs. 9, 10) and juvenile *Micrathena gracilis* showed dark spots under UV light that were not visible under white light (Figs. 7, 8). On average, the abdomen of spiders had a lower UV-brightness (-8) than the cephalothorax (-4).

Reflectance of background vegetation.—

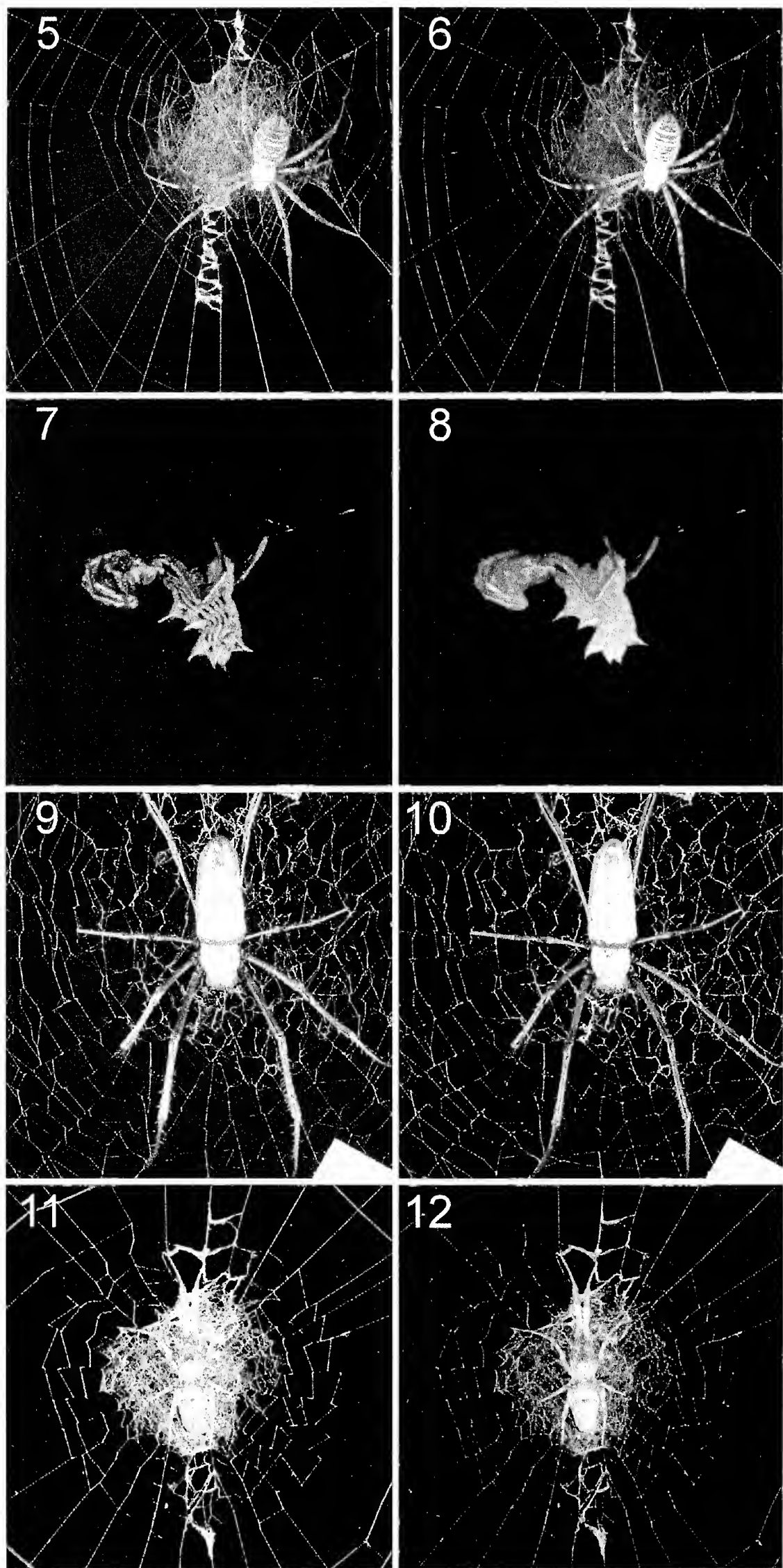
As a control of my approach and to compare reflectance patterns and UV-brightness of flowers with that of spiders and their webs, I photographed nine different flowers and a variety of plants using the same method as I used for spider pictures, albeit with a smaller aperture ($f = 32$).

Stems and leaves generally appeared somewhat darker under UV light than under white light (UV-brightness = -5, Figs. 13–16). The UV-brightness of the flowers varied considerably (Figs. 13, 14). Two flowers (*Geranium sanguineum* and *Echium vulgare*) had a pos-

itive UV-brightness of 20 and 4 respectively, whereas the other seven flowers had a negative UV-brightness ranging from almost neutral (-2, *Barbarea vulgaris*) to -70 (*Leucanthemum vulgare*). Some of the UV-bright to UV-neutral flowers showed dark, distinct patterns under UV light, which are thought to serve as guiding lines for visiting pollinating insects (Figs. 13, 14; Jones & Buchmann 1974).

DISCUSSION

Reflectance of silk.—It is striking, that most silk types showed a very similar UV-brightness of around +10, the only exceptions being sticky (cribellate) and dry silk in uloborid webs, and detritus and egg sac stabilimenta of *Cyclosa* spp. My study thus could confirm that cribellate sticky silk has a higher UV-brightness than ecribellate sticky silk (Craig & Bernard 1990; Craig et al. 1994).



Figures 5–12.—Spiders and central part of their webs photographed under UV light (left) and white light (right): 5, 6. *Argiope bruennichi*; 7, 8. juvenile *Micrathena gracilis*; 9, 10. *Nephila senegalensis*; 11, 12. *Zosis geniculatus*.



Figures 13–16.—Plants under UV light (left) and white light (right). Stems, leaves, and many flowers appear darker under UV light than under white light. The flowers of the dandelion (*Taraxacum officinale*, yellow colored, A), the bloodred cranesbill (*Geranium sanguineum*, purple colored, B), and the winter cress (*Barbarea vulgaris*, yellow colored, C) show distinct, contrasting patterns under UV light, which are thought to serve as guiding lines for visiting pollinating insects. Note that the two flowers that appear white (Oxeye daisy, *Leucanthemum vulgare*, D) or whitish (Clematis, *Clematis* sp., E) to us are among the darkest under UV light. Pictures taken with a smaller aperture than, but otherwise identical set-up as the spider pictures. A colored version of Fig. 14 can be found at <http://faculty.vassar.edu/suter/joaserver/>.

However, my study could not confirm that stabilimenta have a higher UV-brightness compared to other silks in orb-webs (Craig & Bernard 1990). It is not clear why my results differ from those of earlier studies. There are several possible explanations: 1. The difference in UV-brightness between the stabilimenta and other silk types is too small to be detected using photographs. 2. The measurements of Craig & Bernard (1990) and Craig et al. (1994) considered each wavelength separately, whereas the measurements in the present study are integrations over a range of wavelengths. 3. Craig & Bernard 1990 did not consider wavelengths shorter than 340 nm and their measurements suggest that UV reflectance of stabilimenta drops off below 360 nm; whereas measurements in my study consid-

ered wavelengths down to 300 nm (wavelengths < 340 nm may not be very relevant biologically, since few insects are sensitive to wavelengths < 340 nm; Briscoe & Chittka 2001). 4. The reflectance measurements of Craig & Bernard (1990) may have been biased since the diameter of some of the spider's silks (0.4–4 μm ; Craig 1986; Vollrath & Köhler 1996; Zschokke 2000) lies in the range of the wavelengths of visible light (0.4–0.7 μm), and the interactions between light and such thin objects are rather complex (Craig 1988; Nishiyama et al. 2001). 5. Since the reflectance of silk depends on the incident angle of the light (cf. radii in Figs. 11, 12), Craig & Bernard's measurements, which used the same incident angle of light for all measurements, may not be representative, espe-

cially if there is an interaction between the incident angle of light and wavelength. 6. If some silk types are fluorescent, this could result in an over-estimation of their UV reflectance using the method of Craig & Bernard.

Whichever method is used to measure silk reflectance, one conclusion remains the same: all silks in orb-webs (including stabilimenta) reflect more UV light than the background vegetation, which reflects little UV light, and therefore appears darker under UV light (Frolich 1976; Chittka et al. 1994; Figs. 15, 16). However, the analysis presented in this paper shows that the UV-brightness of silk stabilimenta is much smaller than that of some flowers, and it is therefore questionable whether stabilimenta can attract pollinating insects through their UV reflectance.

Reflectance of spiders.—Spiders varied in the way they reflect UV light compared to white light. There seems to be a trend for the more colorful species (e.g., *A. bruennichi*, *A. argentata*, *N. senegalensis*, *V. arenata*) to show a neutral UV brightness, whereas the more cryptic species (e.g., *Arachnura* sp., which tries to mimic a dead leaf, *Micrathena gracilis*, which resembles a ball of dirt) seem to have a lower UV-brightness. One can speculate that the reduced reflectance under UV light, which is comparable to that of the background vegetation, is part of the camouflage of this spider. Due to the simultaneous positive UV-brightness of silk, and the negative or neutral UV-brightness of the spiders, the spiders with a hub stabilimentum appear more cryptic under UV light than under white light (Figs. 5, 11).

Visibility of webs.—The visibility of the web is crucial for the spider: the web should be simultaneously invisible or attractive to the spider's prey and invisible or deterring to the spider's potential predators (Blackledge 1998a). Many of these potential prey or predator species (e.g., insects and birds) are known to have UV receptors (Menzel & Backhaus 1991; Finger & Burkhardt 1994), and consequently, the UV reflectance of spiders and their webs must be considered. At the same time, color perception and spatial resolution of the visual systems of potential prey or predator species must be taken into account.

Insect vision differs fundamentally from that of humans and other vertebrates. First, many insects can detect UV light but few are

sensitive to red (Briscoe & Chittka 2001). Second, insects differentiate colors primarily through their color contrast and not through brightness (Fukushi 1990; Backhaus 1991; Chittka et al. 1992; Chittka et al. 1994). To insects, objects that we perceive as white and that also reflect UV light (i.e., have a flat spectrum), have the same color as the background (e.g., leaves, bark, soil), all appearing achromatic at the center of the insect color space, since insects are not able to detect red light, which we use to distinguish white objects from leaves or soil. As a consequence, there are very few white (i.e., white for humans), insect pollinated flowers that also reflect in the UV wavelengths (Kevan et al. 1996; see also Figs. 13, 14). Silk stabilimenta probably also fall into this category: to humans they appear white and they reflect UV light. We may therefore conclude that stabilimenta, being achromatic, are not very conspicuous to insects (Blackledge 1998a).

Our eyes have a maximum resolution of 0.3 min of arc. To be able to see a typical spider thread with a diameter of two μm with the naked eye would require us to approach it to a distance of less than two cm, at which distance we are not able to focus on it. We can therefore perceive spider threads only if there is a large contrast between the thread and the background compensating for the lack of spatial resolution of our eyes. In a similar way, the apparent size of all fixed stars in the sky at night falls below our eye's resolution, but we can nevertheless perceive many of them, thanks to their great contrast to the dark sky. Since spider silk is white, the best way for us to achieve the necessary high contrast to see single threads, is to view them brightly illuminated against a dark background. The spatial resolution of insect's eyes is roughly 100 times poorer than our own (Wehner 1981), which would require the insects to approach the web to less than a mm to be able to see it. It is not known, how and under what circumstances the insect eyes can make up for the lack of resolution to see spider threads. However, Rypstra (1982) and Craig (1986) have reported that *Drosophila* sometimes change their flight path as they approach silk strands, suggesting that they are able to detect them.

It is not quite certain how insects perceive stabilimenta, which have a fairly flat spectrum

and which could therefore be expected to appear rather dull and colorless to them. In one experiment, Blackledge & Wenzel (2000) found that they could not train bees to associate a reward with stabilimentum silk, whereas they could train bees to associate a reward with silks that have UV reflective peaks. On the other hand, Blackledge & Wenzel (2001) also showed that spiders in stabilimenta decorated webs were more likely to survive attacks of mud-dauber wasps, suggesting that the wasps were able to perceive the stabilimentum.

Bird vision is more similar to that of humans, but it often—like that of insects—extends into the UV (Finger & Burkhardt 1994). Consequently, stabilimenta are probably quite conspicuous to birds. Since birds are only rarely the prey of spiders, it may be concluded that the main function of stabilimentum is probably deterrence against birds, rather than attraction of prey; thus confirming the studies of e.g., Lubin (1975), Horton (1980), Eisner & Nowicki (1983), Schoener & Spiller (1992) and Blackledge & Wenzel (1999). However, before any final conclusions can be drawn, much more must be learned about the way different potential prey and predators perceive spiders and their webs.

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PITFALL TRAPPING IN POPULATION GENETICS STUDIES: FINDING THE RIGHT “SOLUTION”

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ABSTRACT. It is imperative to obtain a representative sample of each population for population genetics studies. Furthermore, it must still be possible to isolate DNA from these organisms. We adapted the pitfall technique for that purpose after encountering severe problems collecting sufficiently large numbers of live *Coelotes terrestris* (Wider 1834) (Amaurobiidae) in the field. Although this species is commonly caught in pitfalls, collecting them by hand proved to be much more laborious than expected. Initially, we tested two types of live-traps (one cup and one funnel trap) which had been successfully used to catch carabid beetles. Both types did not yield enough captures of *C. terrestris* to get a representative sample of the studied populations. Therefore, we tested three different killing/preservative solutions (70 % ethanol, acetic acid + TE buffer and 4% formaldehyde) for possible use in pitfall traps. Ethanol was the best preservative solution based on the amount of DNA that could be isolated after treatment and on the ability to generate the same RAPD profile as a reference DNA sample preserved at -20°C . To test ethanol as a preservative solution in the field, we varied its concentration and used it in combination with traps with or without funnels. We conclude that it is best to use a funnel trap with 96% ethanol. We further recommend that for every new species to be sampled in this way an explorative investigation should be carried out determining where, when, and how many traps should be placed (this reduces the expense of the method). Furthermore, the effects of different preservative solutions on the DNA of an organism of interest should be tested. The resolution of the molecular analysis will determine if the DNA should be of high-molecular-weight or if some degree of denaturation is allowed.

Keywords: Pitfall trapping, DNA preservation, *Coelotes terrestris*, population genetics, Araneae

The possibility of using spiders as bio-indicators for nature conservation measures such as assessing effects of habitat fragmentation was proposed in Maelfait (1996), Maelfait & Baert (1997) and Maelfait & Hendrickx (1998). We are investigating possible population genetic effects from forest fragmentation in Flanders (Belgium) on the spider *Coelotes terrestris* (Wider 1834) (Amaurobiidae). This model organism was chosen because it is strongly bound (stenotopic) to forest habitats based on its way of prey capture and web building (Tretzel 1961). Furthermore, it is one of the most abundant spider species in forests on loamy or sandy loam soils (De Bakker et al. 2000).

It is imperative to obtain a representative sample (e.g., 30 individuals) of each popula-

tion for population genetics studies. Furthermore, it must still be possible to isolate DNA from these organisms. We encountered severe problems during sampling campaigns collecting sufficiently large numbers of live spiders in the field. Although this species is among the most commonly caught spiders in pitfalls, collecting them by hand proved to be much more laborious than expected. Because the spider is night active, it mostly remains hidden during the day in places not easily accessible, making them extremely difficult to find and collect.

It is indeed possible to catch large numbers of *C. terrestris* in a short period of time by means of pitfall traps filled with formaldehyde (Segers & Maelfait 1990). Most individuals are caught from August through October and

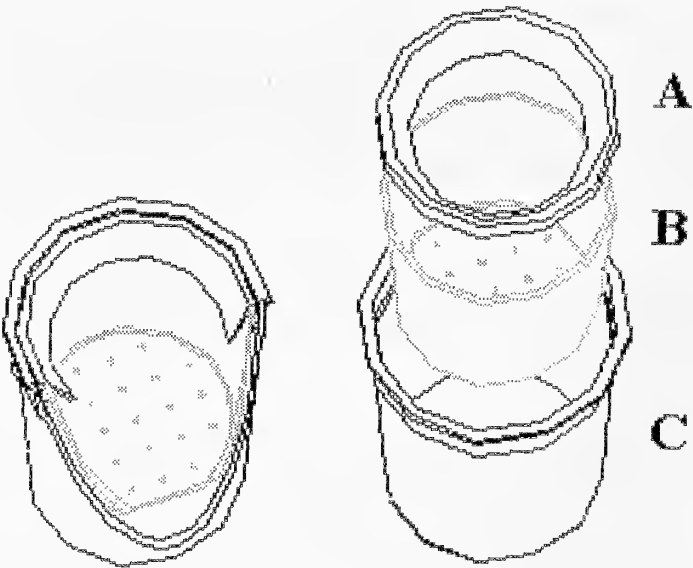


Figure 1.—Pitfall trap Type I (A: plastic rim, B: small receptacle and C: large cylinder) to collect *Coelotes terrestris*.

are adult males actively searching for females. Pitfall traps are commonly used to investigate abundance, activity, and distribution of epigeal arthropods. The method is very attractive because it is not labor-intensive to catch a large amount of organisms and it is inexpensive (Maelfait & Baert 1975; Topping & Sunderland 1992). The possibility to use it for population genetics studies, however, was to our knowledge, never tested.

The challenge of this research was to find (1) a suitable trap type that makes it possible to collect a representative sample of the populations and (2) a trapping solution that does not affect DNA quality. This would strongly reduce the need to use hand catches or even make them superfluous.

METHODS

Description of the traps.—We tested two types of traps. The cup trap (Type I, Fig. 1) was provided by Dr. H.-J. Vermeulen (Netherlands), who used it to collect ground-active carabid beetles. It consists of one large plastic cylinder (diameter 11 cm, 15 cm deep) that, by means of a black plastic rim, holds a small plastic receptacle to collect the organisms (10 cm diameter, 9.5 cm depth, with small drainage holes for the rain water). The trap was used as a live-trap and was one-fifth filled with dead leaves to create hiding places. We sampled 10 forests with 9 traps that were 3 m apart and in a square of 6 by 6 m. The traps were used in August and September 1999 and were emptied every fortnight.

The Type II trap consists of a plastic bottle

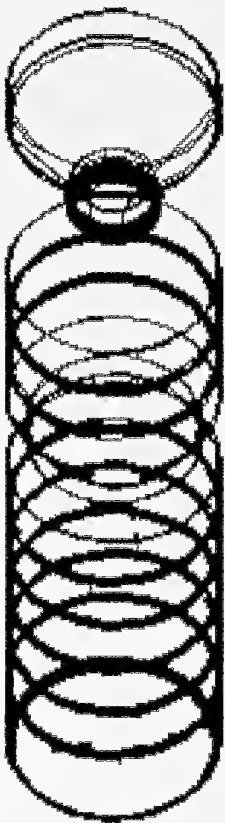


Figure 2.—Pitfall trap Type II & III: plastic water bottle with cut-off top to collect *Coelotes terrestris*.

with a cut-off top (diameter 7.5 cm, depth 20 cm, Fig. 2) and was one-third filled with ethanol. In the Type III trap we used the cut-off top as a funnel in the plastic bottle. The funnel-neck had a diameter of 2.5 cm. The funnel trap was used as a live-trap and half-filled with dead leaves to create hiding places for the captured organisms (Type IIIa). It was also used in combination with ethanol (Type IIIb).

From August to October 2000, 16 sites in 13 forests were sampled with 3 traps that were 3 m apart. The different trap types and solutions were tested consecutively during the sampling campaign (Table 1). The traps were emptied weekly.

All traps were placed in the interior of the

Table 1.—Scheme of the *Coelotes terrestris* sampling campaign. Each week, sixteen sites were sampled with 3 traps per site.

Week	Date
1	Type IIIa
2	Type IIIa
3	Type IIIa
4	Type IIIb-96% ethanol
5	Type IIIb-96% ethanol
6	Type II-96% ethanol
7	Type II-75% ethanol
8	Type II-85% ethanol

forest, under the trees. They were sunk in the ground with their rim level to the soil surface. About 3 cm above each trap was a 15x15 cm PVC roof to guard it from excessive rain, leaves or other debris. There were also plastic strips (height 3 cm, length 25 cm) on two opposing sides of the trap to guide the spiders into the trap.

All investigated forests were deciduous and mainly beech (*Fagus sylvatica*) forests, occurring on sandy loam or loamy soils and with a litter layer of the *moder*-type. They are old forests occurring on the maps of De Ferraris (1772–1779), the oldest topographical maps of Flanders. The choice of sampling sites in the forest was based on an earlier inventory study by De Bakker et al. (2000).

Testing preservation solutions.—We used eight individuals of *C. terrestris* to test three solutions: 70% ethanol (diluted from 96% ethanol), a 1:1 mixture of acetic acid:TE buffer (Tris + EDTA) and 4% formaldehyde. For each individual, one pair of legs was kept in 1 ml of each of the three solutions for 2 months at room temperature. The fourth pair of legs was stored at -20°C as a control sample.

Formaldehyde and acetic acid + TE (derived from Carnoy's solution: 60% ethanol, 30% chloroform, 10% acetic acid, pH 2.6) were tested as less expensive alternatives to ethanol. We especially wanted to test the short-term storage effect of these solutions on the DNA of *C. terrestris*.

Genomic DNA was extracted with the PureGene DNA isolation kit (Type D-5000A, Gentra Systems, Inc., Biozym, Landgraaf, The Netherlands), following the manufacturer's instructions. The isolated DNA was quantified with a spectrophotometer and brought to a final concentration of 5 ng/ μl for further analysis. The RAPD technique (Random Polymorphic DNA, Welsh & McClelland 1990; Williams et al. 1990) was conducted as described in Gurdebeke et al. (2000) with primer OPA-01 (Operon Technologies Inc., Alameda, California, USA) to check the quality of the isolated DNA.

Testing ethanol in the field.—To test ethanol as a preservative solution in the field, we varied its concentration (96%, 85% and 75%) and used it in combination with traps without (Type II) or with a funnel (Type IIIb). All dilutions of ethanol were made from a non-de-

natured 96% stock solution. The traps were emptied every week and the organisms were kept in 70% ethanol at -20°C prior to DNA isolation. The DNA was isolated within one month after catching the spiders and the quality was checked during a 0.8% agarose gel electrophoresis.

For every sampling site, the proportion of *C. terrestris* caught with Type II, Type IIIa and Type IIIb traps was calculated. By using proportions, we can correct for differences in abundance between different sampling sites. To correct for possible phenology-related differences in the number of caught individuals, we only used the data of week 3 (Type IIIa), 5 (Type IIIb) and 6 (Type II). A non-parametric Friedman ANOVA tested for significant differences in capturing rates between the trap types (StatSoft, Inc. 2000).

Voucher specimens were deposited in the Royal Belgian Institute of Natural Sciences in Brussels, Belgium (identification number IG 29.487).

RESULTS

Live-traps.—Although very suitable for trapping carabid beetles (Vermeulen 1994), the cup traps filled with leaves (Type I) yielded fewer than 10 *C. terrestris* in all traps in the 10 forests where the traps were used. The funnel trap filled with leaves (Type IIIa) gave variable results. In only one of the sixteen sampling sites, a representative sample of the population (being at least 30 individuals) was caught in 3 weeks, but no individuals were captured in 13 of the sampling sites. Despite the leaves, occasional killing still occurred when more than one spider was caught in one trap. These results made it necessary to investigate the possibility of using a fluid in the pitfall traps that would preserve the DNA of the captured spiders.

Preservation solutions.—Spectrophotometric quantification of the DNA showed that no DNA could be isolated from the samples stored in acetic acid + TE buffer (Table 2). During DNA isolation, we also noticed that those legs were more brittle than legs stored in other solutions. The samples stored in ethanol and formaldehyde both yielded sufficient DNA, however, the amount of isolated DNA was lower than that isolated from legs that were kept at -20°C . The quality of the DNA was assessed after subjecting the samples to

Table 2.—Amount of isolated *Coleotes terrestris* DNA after different treatments (* isolation failed).

Individual	Control (−20°C) (ng/μl)	70% ethanol (ng/μl)	4% formaldehyde (ng/μl)	Acetic acid + TE (ng/μl)
1	65.50	90.25	12.00	0
2	76.00	74.25	314.25	0
3	111.50	10.75	21.00	0
4	113.00	—*	34.75	0
5	222.50	82.00	4.25	0
6	187.00	30.00	25.75	0
7	116.00	36.25	3.25	0
8	142.00	99.75	8.00	0
Mean	129.19	60.46	52.91	0
st.d.	53.25	34.33	106.17	0

RAPD analysis. It was impossible to generate a RAPD profile from the samples kept in formaldehyde, while the samples stored in 70% ethanol yielded the same banding profile as the control sample that was kept at −20 °C (Fig. 3).

Testing ethanol in the field.—The performance of the traps was evaluated based on the following criteria: the efficiency of the trap (catching and retaining a sufficient number of organisms) and the ability to preserve DNA so that no degradation takes place. We include the live-trap of Type IIIa again in the interpretation of these results. Friedman ANOVA proved the capture rates of the three trap types being significantly different ($P < 0.0001$; Fig. 4).

Live-traps with funnels (Type IIIa) caught

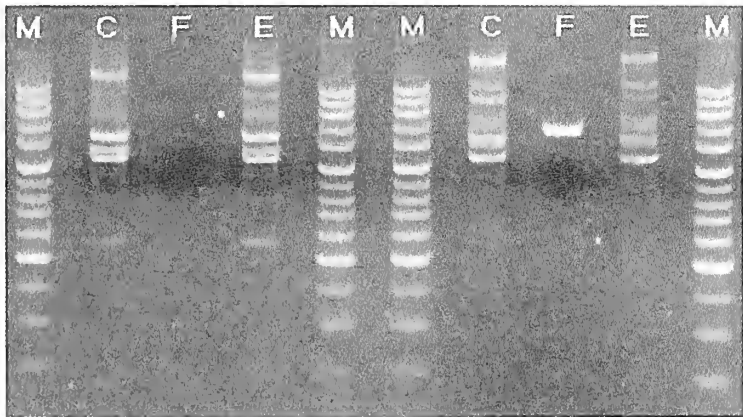


Figure 3.—Banding profiles of 2 *Coelotes terrestris* individuals, generated by RAPD with primer OPA-01 after the different treatments (M: molecular marker, C: control−20 °C, F: formaldehyde, E: 70 % ethanol). It was impossible to generate a RAPD profile from the samples kept in formaldehyde, while the samples stored in 70% ethanol yielded the same banding profile as the control sample that was kept at −20 °C.

on average $5.92 \pm 3.29\%$ of the individuals. They were the least efficient with regard to the number of captured organisms. In contrast, DNA of the few animals that were caught alive in these traps and then stored at −20 °C was well preserved and was always of high molecular weight. Funnel traps filled with ethanol (Type IIIb, 96% ethanol) caught more individuals ($32.66 \pm 6.19\%$) and DNA quality of the spiders was good and showed no degradation (Fig. 5). The most individuals ($61.42 \pm 6.67\%$) were caught with ethanol traps without funnels (Type II, 96% ethanol). However, these traps did not preserve the DNA well enough to yield non-degraded high-molecular-weight DNA.

The DNA of organisms caught with traps filled with 85% and 75% ethanol was also not well-preserved and yielded no or totally degraded DNA.

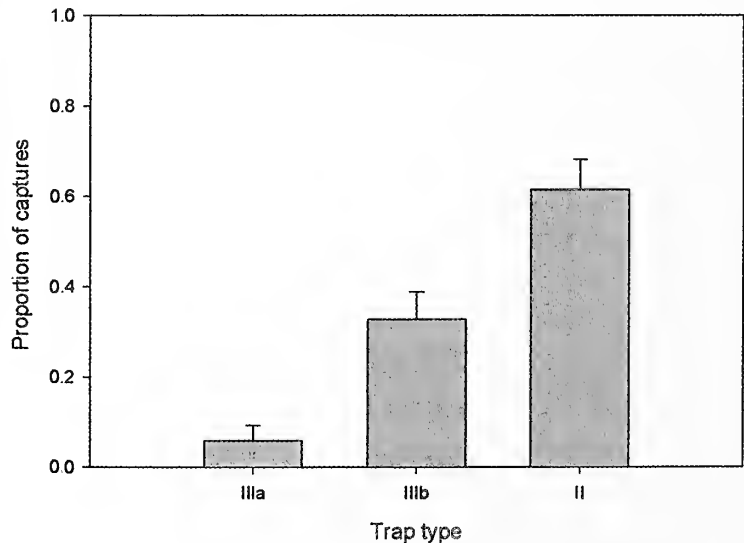


Figure 4.—Proportion of *Coelotes terrestris* captures in traps of Type II, IIIa and IIIb. Capture results are significantly different between the three trap types (Friedman ANOVA, $P < 0.0001$).

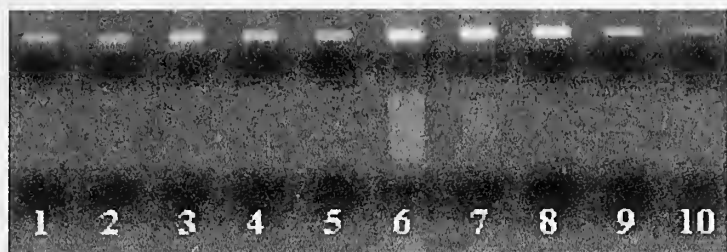


Figure 5.—Quality of isolated *Coelotes terrestris* DNA caught in pitfall traps with funnel and 96% ethanol. Each track represents total genomic DNA of high molecular weight from one individual.

DISCUSSION

Live-traps.—We first tried dry traps because these capture animals alive to be subsequently frozen to preserve their DNA for further molecular-genetic analysis. None of the two live-traps yielded enough organisms to get a representative sample of the studied populations. This was probably due to a high escape rate of the spider from the trap. Linyphiid spiders may escape from (even fluid-filled) pitfall traps (Topping 1993), but this remains an open question for *C. terrestris*. Adding a fluid to the trap prevents spiders from escaping, making the trap more efficient (Curtis 1980; Topping & Luff 1995). This was also observed in this study.

The cup traps caught fewer animals than funnel traps. Obrist & Duelli (1996) recommended funnel traps to collect epigeal arthropods, because they are more efficient than cup traps. The funnel was said to lower the incidence of escape. The small depth might also cause the disappointing results of our cup traps. Adis (1979) recommends traps at least 12 cm deep.

Another factor that might influence the escape from the dry traps is that the traps are made of plastic. Re-using plastic traps roughens the trap surface and may affect the capture (and maybe also the retaining) efficiency of the trap (Topping & Luff 1995). According to Luff (1975) and Waage (1985), escape from empty plastic traps is higher than from empty glass traps for beetles. This is presumably also the case for ground-active spiders.

Preservation solutions.—Degradation of DNA occurs when endo- and exonuclease activity cleaves the DNA strand and breaks it up in small fragments which are no longer suitable for further molecular analysis (Linn 1981). Ester linkages with phosphate molecules and carbon–nitrogen linkages are espe-

cially susceptible to modifications in DNA (Cann et al. 1993). Storing samples at -20°C or -80°C can inhibit the activity of the nucleases. This method is very cheap and fast and therefore the most widely used. However, some research has also been done to preserve DNA in a chemical solution (see below).

In this study, ethanol was found to be the best chemical preservative based on the amount of DNA isolated after treatment and the ability to generate the same RAPD profile as a reference DNA sample preserved at -20°C . Animal tissue DNA preserved in ethanol may give successful PCR amplification (Dessauer et al. 1996; Dick et al. 1993), but substantial degradation for spider DNA was found after storage for three weeks in 70% ethanol and ethylene glycol at room temperature (A'Hara et al. 1998). This degradation was also reported by Seutin et al. (1991), Holzmänn & Pawlowski (1996) and Zhang & Hewitt (1998).

Acetic acid with TE buffer, the solution derived from Carnoy's fixative (60% ethanol, 30% chloroform, 10% acetic acid, pH 2.6) gave the worst results of the three tested solutions. It was impossible to isolate DNA from the legs stored in this fixative. Disappointing results with Carnoy's fixative were also reported by Post et al. (1993) and Koch et al. (1998). It is however possible to use Carnoy's fixative when only specific target sequences need to be amplified from fixed tissues (Honma et al. 1993; Li et al. 1995).

The negative effect of formaldehyde on DNA found by others (Dessauer et al. 1996; Jackson et al. 1991; Holzmänn & Pawlowski 1996) was also observed in this study. This can explain why no or only a strongly reduced RAPD banding profile was found, since the RAPD technique needs non-degraded, high-molecular-weight DNA. In contrast, buffered formalin gave good results for targeting specific sequences (Honma et al. 1993) or for the extraction of high-molecular-weight DNA for Southern blot analysis (Koshiba et al. 1993).

A variety of preservation solutions have been tested, sometimes with contradictory results. Seutin et al. (1991) recommended saline solutions; Fukatsu (1999) had good results with 2-propanol (but Post et al. (1993) did not), ethyl acetate (but Reiss et al. (1995) did not) diethyl ether and acetone. Methanol (Post et al. 1993; Fukatsu 1999) and chloroform

(Fukatsu 1999) showed poor DNA preservation. Thus, contradictory findings exist concerning which specific solution is good for DNA preservation. One should test the effect of a particular DNA fixative on the organism of interest before using it as a storage medium. The resolution of the molecular analysis will determine if the DNA should be of high-molecular-weight or if some degree of denaturation is allowed.

Testing ethanol in the field.—One has to consider two aspects when using ethanol as a preservative solution in the field: the high evaporation rate of this solution and the expense of using (nearly) absolute ethanol. An ethanol concentration of 70% proved to have enough preservative capacities in the lab. However, when 75% or even 85%, was used in the field, the DNA of the spiders showed massive degradation. It seems that a certain threshold concentration is necessary to prevent the DNA from losing its original structure. The concentration of 70% or 85% ethanol probably became diluted through evaporation in the field, causing it to lose its preservative properties. Using both concentrations in a trap with a funnel to minimize evaporation gave no better results.

When using absolute ethanol in the field (96%), we did see an effect of using a funnel trap to prevent evaporation. Although the DNA of spiders caught in cup traps filled with 96% ethanol was not intact, the DNA of those captured in funnel traps was. Therefore, we conclude that it is best to use a funnel trap with 96% ethanol.

It is recommended that for every new species to be sampled in this way an explorative investigation should be carried out determining where, when, and how many traps should be placed (this reduces the expense of the method). Furthermore, the effects of different preservative solutions on the DNA of an organism of interest should be tested.

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GROUND-LIVING SPIDERS IN BOGS IN NORTHERN EUROPE

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ABSTRACT. Spiders were studied in open *Sphagnum* bogs in Sweden, Finland and northern Norway. Material was collected in pitfall traps. Southern sites (hemiboreal zone) differed from coniferous taiga sites (boreal zone, including three subzones), and also the northern sites, north of taiga (palsa and hemiarctic zones) had their own fauna. Typical abundant species for hemiboreal zone was *Pirata uliginosus*, for boreal zone(s) *Pardosa sphagnicola* and *P. hyperborea* and for palsa and hemiarctic zones *Hilaira nubigena* and *Pardosa atrata*. No species was found to be dominant and typical throughout the study area.

Keywords: Bogs, abundant spiders, North Europe, Araneae

Peatlands (bogs, fens, mires) are typical habitats in northern Europe, especially in the boreal (taiga) zone (e.g. Eurola et al. 1984). For example, about 30% of the land area of Finland was still classified as peatlands in the 1950's; of this about half has now been changed by human activities; forestry, agriculture and peat harvesting (Wahlström et al. 1996). Although natural peatlands can still be found in northern Europe, in contrast to Central Europe, many organisms living in bogs are now considered endangered. This is true for spiders, e.g., six (or 17.5%) of the 34 spider species included in the Red Data Book of Finland are bog-dwellers (cf. Koponen 2002). The same proportion (17.5%) of the 63 spiders in the Red Data Book of Sweden live in wetlands (bogs or shores of freshwaters) (Gärdenfors 2000).

Although the local spider faunas of bogs in northern Europe have been studied in many countries, only Krogerus (1960), Vilbaste (1980–81) and Koponen et al. (2001) have presented more general analyses of the northern bog fauna. Krogerus (1960) dealt with all arthropods in bogs in Fennoscandia (i.e., Finland, Sweden, Norway and westernmost parts of north Russia); the data on spiders are, due to collecting methods and some taxonomic problems, a little out-of-date when compared with the above-mentioned studies.

In the present paper, I focus on the ground-living spider species in open treeless bogs (*Sphagnum-Eriophorum-Carex* bogs) in different vegetation/bog zones of Finland, Swe-

den and northernmost Norway, east of the Scandian Mountain Range. Main attention is paid to the common (abundant and typical) spider species.

METHODS

The study sites, 31 bogs, are shown in Table 1. Seven sites are situated in hemiboreal, six in southern boreal, five in middle boreal, five in northern boreal, four in palsa bog (see Eurola et al. 1984) and four in hemiarctic coastal bog zone (see also Fig. 1). All study bogs are situated east of the Scandian Mountain Range (located on the border between Norway and Sweden) at low level, the maximum elevation is 500 m (Varsångssjön site in Sweden). All study sites are situated on the mainland, the Baltic Sea islands being excluded from this paper, due to the special composition of bog spider faunas on islands (e.g., Lehtinen et al. 1979; Almquist 1984; Koponen 2002).

The open peat bogs studied are characterized by *Sphagnum* mosses, cottongrass (*Eriophorum*), sedge (*Carex*) species and cloud-berry (*Rubus chamaemorus*). In addition, low shrubs (*Calluna*, *Ledum*, *Andromeda*, *Betula nana*) and sometimes small pines (*Pinus sylvestris*) are found.

The collecting method was pitfall trapping, 50 traps were used in Karevansuo, 20 traps at other sites. The traps were glass or plastic cups (diameter ca. 6 cm, depth 8 cm) with an aluminium cover to protect traps from rainfall and litter. The preservation liquid was ethylene glycol with some detergent. The distance between traps was 2–3 m, and they were

Table 1.—Study sites in northern Europe; abbreviations for countries and for vegetation zones F = Finland, N = Norway, S = Sweden, I = hemiboreal, II = southern boreal, III = middle boreal, IV = northern boreal, V = palsa bogs, VI = hemiarctic coastal bogs; see Fig. 1.

Bog (parish/area)	Country	Zone	Latitude (N)	Study year
1. Vissmosse (Hörby)	S	I	55°50'	1969
2. Store mosse (Värnamo)	S	I	57°15'	1969
3. Skagershulta (Örebro)	S	I	59°00'	1977
4. Filipstad (Filipstad)	S	I	59°42'	1977
5. Sammalsuo (Halikko)	F	I	60°20'	1970
6. Karevansuo (Masku)	F	I	60°32'	1960's
7. Rehtsuo (Vahto)	F	I	60°35'	1976
8. Stackmora (Orsa)	S	II	61°05'	1977
9. Losemyra (Söderhamm)	S	II	61°25'	1977
10. Kirstula (Renko)	F	II	60°55'	1977
11. Siikaneva (Ruovesi)	F	II	61°52'	1978
12. Haapasuo (Leivonmäki)	F	II	61°54'	1978
13. Lehmo (Kontiolahti)	F	II	62°40'	1970
14. Brana (Östersund)	S	III	63°05'	1977
15. Torsmyra (Umeå)	S	III	63°35'	1977
16. Niemisvesi (Ähtäri)	F	III	62°33'	1969
17. Hirvisuo (Pudasjärvi)	F	III	65°20'	1977
18. Yli-Ii (Ii)	F	III	65°25'	1977
19. Varsångssjön (Östersund)	S	IV	63°06'	1977
20. Vilhelmina (Vilhelmina)	S	IV	64°37'	1977
21. Torankijärvi (Kuusamo)	F	IV	65°58'	1967
22. Hanhimaa (Kolari)	F	IV	67°15'	1978
23. Säytsjärvi (Inari)	F	IV	69°20'	1969
24. Perkosvuoma (Kiruna)	S	V	67°50'	1971
25. Puksalansuo (Utsjoki)	F	V	69°44'	1969
26. Vaisjäggi (Utsjoki)	F	V	69°49'	1977
27. Varangerbotn (Nesseby)	N	V	70°10'	1971
28. Mortensnes (Nesseby)	N	VI	70°10'	1973
29. Kiby (Vadsö)	N	VI	70°05'	1973
30. Vieksajokka (Porsanger)	N	VI	70°22'	1978
31. Simplevatn (Tana)	N	VI	70°25'	1978

placed in lines. Material was collected in the 1960's–1970's (Table 1) by the author. The trapping period was the summer (or growing) season (i.e., 5 months in the south and 2.5 months in the north). The traps were emptied usually once a month. Only one site (Karevansuo in Finland) was studied during three summers, the others were trapped during one summer.

The usefulness of pitfall traps in community studies has been discussed by many authors (e.g., Curtis 1980; Norris 1999). They are suitable for collecting at least common and typical ground-dwelling spider species in a given habitat, especially if trapping is done by the same person. One year of trapping seems to be adequate to find the typical spider species of bogs, despite year to year dif-

ferences (cf. Relys et al. 2002). Dominant and typical species for each zone are listed (Table 3) after average dominance rank, for example if a species was 1st, 2nd, 2nd, 3rd, 3rd and 1st in abundance in six bogs, its average dominance rank in this zone is (12/6) = 2.0. The species listed as dominants in a bog zone (Table 3) were found at all bog sites of that zone.

The present material includes 17,360 identified specimens, material is deposited in the Zoological Museum, University of Turku. Nomenclature is according to Platnick (1997) with a few exceptions (*Tricca/Arctosa* and *Agyneta/Meioneta*).

RESULTS

A case study.—The most abundant species, and some rare interesting ones, found in the

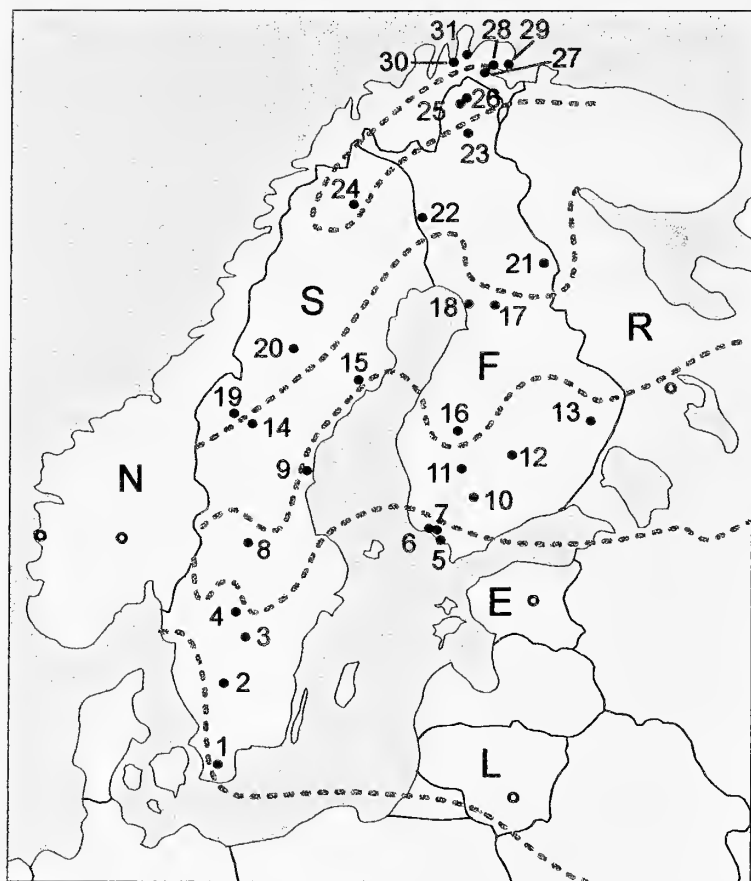


Figure 1.—Study bogs (1–31) and vegetation zones, indicated by dotted lines (modified from Ahti et al. 1968) in northern Europe. Sites 1–7 in hemiboreal, 8–13 in southern boreal, 14–18 in middle boreal, 19–23 in northern boreal, 24–27 in palsa bog and 28–31 in hemiarctic coastal zone, see Table 1. Open circles = comparative data from literature, see the text. Abbreviations for countries: E = Estonia, F = Finland, L = Lithuania, N = Norway, R = Russia, S = Sweden.

most thoroughly studied bog, Karevansuo in Finland, are shown in Table 2. Spiders in this bog, situated near the northern limit of the hemiboreal zone, were collected during three summers. Two species (*Pirata uliginosus* (Thorell 1856) and *Pardosa hyperborea* (Thorell 1872)) clearly dominated, and the ten most abundant species comprised 69% of all material. Among the 20 most abundant species were nine Lycosidae, nine Linyphiidae, one Hahniidae and one Philodromidae species.

Dominant species.—The dominant species in each vegetation zone are shown in Table 3. Three boreal zones (southern, middle and northern boreal) had the same two top-scorer species *Pardosa sphagnicola* (Dahl 1908) and *P. hyperborea*, also *Tricca alpigena* (Dolleschall 1852) was typical in boreal zones. In the southernmost, hemiboreal zone, *Pirata uliginosus* and also *Pardosa pullata* (Clerck 1757) were characteristic species. In two northern-

most zones, palsa and coastal hemiarctic bogs, *Hilaira nubigena* (Hull 1911) and *Pardosa atrata* (Thorell 1873) were typical species. There were no species dominant in all studied six zones, or even in three zones (if boreal ones are combined). The total number of top-scorers (Table 3) was 20, of which nine were lycosids and eight were linyphiids. A general trend was the dominance of lycosid species in hemiboreal and boreal zones (I–IV), and of linyphiids in palsa and especially in coastal hemiarctic bogs (V–VI).

DISCUSSION

Although the material was collected 20–35 years ago, the spider assemblages are very probably still living in these bogs; bogs are known to be stable habitats under natural conditions (e.g., Karofeld 1995).

When comparing the present data with material from adjacent areas, great faunal similarity (the same abundant species) was found with closely situated bogs in Russian Karelia (near Lake Onega) where the typical boreal bog fauna was reported by Uzenbaev (1987). In the Baltic states, Estonia and Lithuania, fauna generally resembling that in hemiboreal and southern boreal sites of Finland and Sweden was found; however, with some marked differences (Koponen et al. 2001). The present data were more similar with that from Estonia (Vilbaste 1980–81) than with Lithuanian data. For example, the dominant species in Lithuanian peatbogs (Koponen et al. 2001), the lycosid *Aulonia albimana* (Walckenaer 1805), was absent in all present study areas. West of the Scandian Mountain Range, in southern Norway, bog fauna found in continental mountain areas (Hauge & Wiger 1980) partly resembled that of the present study; however, some typical species were missing (e.g., *Pirata uliginosus* and *Gnaphosa lapponum* (L. Koch 1866)). The spider fauna in coastal bogs in southwestern Norway (Pommeresche 1999), differed more from the present one, especially the lycosid fauna (*Pardosa hyperborea* and *P. sphagnicola* missing, and *Pirata hygrophilus* Thorell 1872 dominating).

In general, different vegetation zones had characteristic spider communities. The most southern (hemiboreal) and northern zones (hemiarctic and also palsa zone in lesser degree) differed from the three boreal zones. The border between boreal and palsa zones is

Table 2.—The most abundant species (>10 individuals), and some other interesting bog species, found in Karevansuo bog, Finland; *n* = total number of individuals, *s* = total number of species.

	Family	Inds.	%
<i>Pirata uliginosus</i> (Thorell 1856)	Lycosidae	885	24.1
<i>Pardosa hyperborea</i> (Thorell 1872)	Lycosidae	802	21.9
<i>Tricca alpigena</i> (Doleschall 1852)	Lycosidae	159	4.3
<i>Trochosa spinipalpis</i> (F.O.P.—Cambridge 1895)	Lycosidae	116	3.2
<i>Agyneta cauta</i> (O.P.—Cambridge 1902)	Linyphiidae	112	3.1
<i>Walckenaeria antica</i> (Wider 1834)	Linyphiidae	110	3.0
<i>Pardosa sphagnicola</i> (Dahl 1908)	Lycosidae	99	2.7
<i>Alopecosa pulverulenta</i> (Clerck 1757)	Lycosidae	93	2.5
<i>Macrargus carpenteri</i> (O.P.—Cambridge 1894)	Linyphiidae	85	2.3
<i>Lepthyphante angulatus</i> (O.P.—Cambridge 1881)	Linyphiidae	80	2.2
<i>Antistea elegans</i> (Balckwall 1841)	Hahniidae	55	1.5
<i>Maro lepidus</i> Casemir 1961	Linyphiidae	55	1.5
<i>Drepanotylus uncatus</i> (O.P.—Cambridge 1873)	Linyphiidae	49	1.3
<i>Pirata piscatorius</i> (Clerck 1757)	Lycosidae	47	1.3
<i>Centromerita concinna</i> (Thorell 1875)	Linyphiidae	46	1.3
<i>Pardosa pullata</i> (Clerck 1757)	Lycosidae	42	1.1
<i>Pirata insularis</i> Emerton 1885	Lycosidae	38	1.0
<i>Thanatus formicinus</i> (Clerck 1757)	Philodromidae	34	0.9
<i>Agyneta affinis</i> (Kulczynski 1898)	Linyphiidae	34	0.9
<i>Bathypantes gracilis</i> (Blackwall 1841)	Linyphiidae	33	0.9
<i>Stemonyphantes lineatus</i> (Linnaeus 1758)	Linyphiidae	33	0.9
<i>Gnaphosa lapponum</i> (L. Koch 1866)	Gnaphosidae	30	0.8
<i>Drassodes pubescens</i> (Thorell 1856)	Gnaphosidae	26	0.7
<i>Robertus arundineti</i> (O.P.—Cambridge 1871)	Theridiidae	21	0.6
<i>Tallusia experta</i> (O.P.—Cambridge 1871)	Linyphiidae	20	0.5
<i>Bolyphantes luteolus</i> (Blackwall 1833)	Linyphiidae	20	0.5
<i>Agroeca proxima</i> (O.P.—Cambridge 1871)	Liocranidae	19	0.5
<i>Lepthyphantes mengei</i> Kulczynski 1887	Linyphiidae	18	0.5
<i>Haplodrassus signifer</i> (C.L. Koch 1839)	Gnaphosidae	17	0.5
<i>Scotina palliardi</i> (L. Koch 1881)	Liocranidae	15	0.4
<i>Zelotes latreillei</i> (Simon 1878)	Gnaphosidae	15	0.4
<i>Agroeca brunnea</i> (Blackwall 1833)	Liocranidae	13	0.4
<i>Walckenaeria nudipalpis</i> (Westring 1851)	Linyphiidae	13	0.4
<i>Dipoena prona</i> (Menge 1868)	Theridiidae	12	0.3
<i>Bathypantes parvulus</i> (Westring 1851)	Linyphiidae	11	0.3
<i>Centromerus arcanus</i> (O.P.—Cambridge 1873)	Linyphiidae	11	0.3
<i>Xysticus lineatus</i> (Westring 1851)	Thomisidae	7	
<i>Neon valentulus</i> Falconer 1912	Salticidae	6	
<i>Minicia marginella</i> (Wider 1834)	Linyphiidae	6	
<i>Zora parallela</i> Simon 1878	Zoridae	5	
<i>Haplodrassus moderatus</i> (Kulczynski 1897)	Gnaphosidae	5	
<i>Drassyllus pusillus</i> (C.L. Koch 1833)	Gnaphosidae	4	
<i>Pelecopsis parallela</i> (Wider 1834)	Linyphiidae	3	
<i>Taranucnus setosus</i> (O.P.—Cambridge 1863)	Linyphiidae	3	
<i>Pirata piraticus</i> (Clerck 1757)	Lycosidae	2	
<i>Theonoe minutissima</i> (O.P.—Cambridge 1879)	Theridiidae	2	
<i>Gnaphosa microps</i> Holm 1939	Gnaphosidae	1	
<i>Maro sublestus</i> Falconer 1915	Linyphiidae	1	
<i>Maro minutus</i> O.P.—Cambridge 1906	Linyphiidae	1	
<i>Centromerus levitarsis</i> (Simon 1884)	Linyphiidae	1	
<i>Agyneta mossica</i> (Schikora 1993)	Linyphiidae	1	
<i>Walckenaeria capito</i> (Westring 1861)	Linyphiidae	1	
Total <i>n</i> = 3670, <i>s</i> = 98			

Table 3.—Dominant species in peatbogs in different zones (average dominance rank, see Methods).

I. Hemiboreal zone (7 bogs):	
<i>Pirata uliginosus</i>	4.6
<i>Antistea elegans</i>	6.9
<i>Alopecosa pulverulenta</i>	7.0
<i>Pardosa pullata</i>	8.3
<i>Trochosa spinipalpis</i>	10.1
<i>Walckenaeria antica</i>	10.4
II. Southern boreal zone (6 bogs)	
<i>Pardosa sphagnicola</i>	2.0
<i>P. hyperborea</i>	6.5
<i>Antistea elegans</i>	6.8
<i>Pirata uliginosus</i>	7.0
<i>Tricca alpigena</i>	8.5
<i>Alopecosa pulverulenta</i>	10.5
<i>Trochosa spinipalpis</i>	10.8
III. Middle boreal zone (5 bogs)	
<i>Pardosa sphagnicola</i>	1.4
<i>P. hyperborea</i>	2.2
<i>Tricca alpigena</i>	5.0
<i>Antistea elegans</i>	7.2
<i>Alopecosa pulverulenta</i>	7.6
<i>Walckenaeria antica</i>	9.6
<i>Gnaphosa lapponum</i>	11.0
IV. Northern boreal zone (5 bogs)	
<i>Pardosa hyperborea</i>	4.0
<i>P. sphagnicola</i>	8.0
<i>Centromerus arcanus</i>	10.6
<i>Tricca alpigena</i>	11.2
<i>Walckenaeria nudipalpis</i>	14.0
<i>Lepthyphantes angulatus</i>	14.2
<i>Pardosa atrata</i>	16.2
V. Palsa zone (4 bogs)	
<i>Hilaira nubigena</i>	3.8
<i>Pardosa atrata</i>	4.0
<i>P. hyperborea</i>	4.8
<i>Lepthyphantes angulatus</i>	6.3
<i>Tricca alpigena</i>	12.2
<i>Hahnia ononidum</i> Simon 1875	13.0
VI. Hemiarctic coastal zone (4 bogs)	
<i>Hilaira nubigena</i>	3.3
<i>Bathyphantes gracilis</i>	5.0
<i>Pardosa atrata</i>	9.0
<i>Lepthyphantes angulatus</i>	9.0
<i>Agyneta mossica</i>	9.7
<i>Pelecopsis mengei</i> (Simon 1884)	11.0
<i>Pardosa palustris</i> (Linnaeus 1758)	12.5

clear, and it is especially characterized by the high dominance of the linyphiid *Hilaira nubigena* Hull 1911, while in all more southern zones, two or three lycosids were the most abundant species. The great number of species and abundance of linyphiids in the north (and at high elevations) is a known phenomenon (e.g., Koponen 1993). The generalized division, widely used by geobotanists (cf. Ahti et al. 1968), into hemiboreal, boreal and northern (north of taiga forest zone) zones is supported by data on spider faunas. The general correspondence of spider faunas in bogs with vegetation zones has been earlier shown by the author (Koponen 1994) in Quebec, and also in smaller scale in bogs of southwestern Finland (Koponen 2002).

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FINE STRUCTURE OF MALE GENITAL SYSTEM AND SPERM IN SOLIFUGAE DOES NOT SUPPORT A SISTER-GROUP RELATIONSHIP WITH PSEUDOSCORPIONES (ARACHNIDA)

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ABSTRACT. Comparative spermatology may provide characteristics that can be useful in systematics. Previous observations on sperm structure of the solifugid *Eusimonia mirabilis* revealed that the most similar arachnid sperm cells are found within the Actinotrichida (Acari). The general morphology of the testis and the tendency to form sperm aggregates are also similar in both taxa. Since knowledge of sperm in Solifugae until now came only from one species, in contrast to Acari in which all the higher taxa have been investigated, these characters were difficult to assess with regard to systematical implications. The present paper confirms the derived, simple-aflagellate structure of sperm in Solifugae and the similarity with sperm of Actinotrichida, presenting results for two further species of another family (Ammotrechidae) from Argentina. Sperm cells of representatives of both taxa are small, devoid of a flagellum, contain a chromatin body that is penetrated and surrounded by circles of the acrosomal filament, and have a tendency to form peripheral protuberances. Sperm morphology does not support the frequently suggested sister-group relationship between Solifugae and Pseudoscorpiones.

Keywords: Arachnid sperm, comparative spermatology, sperm aggregates, systematics

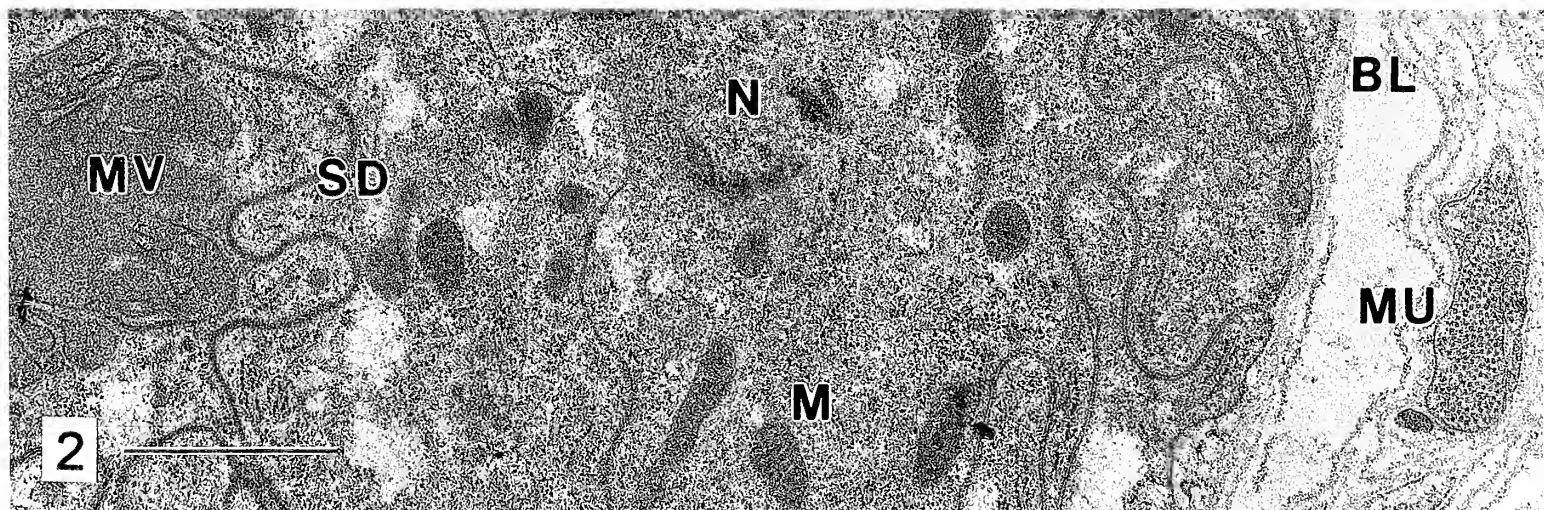
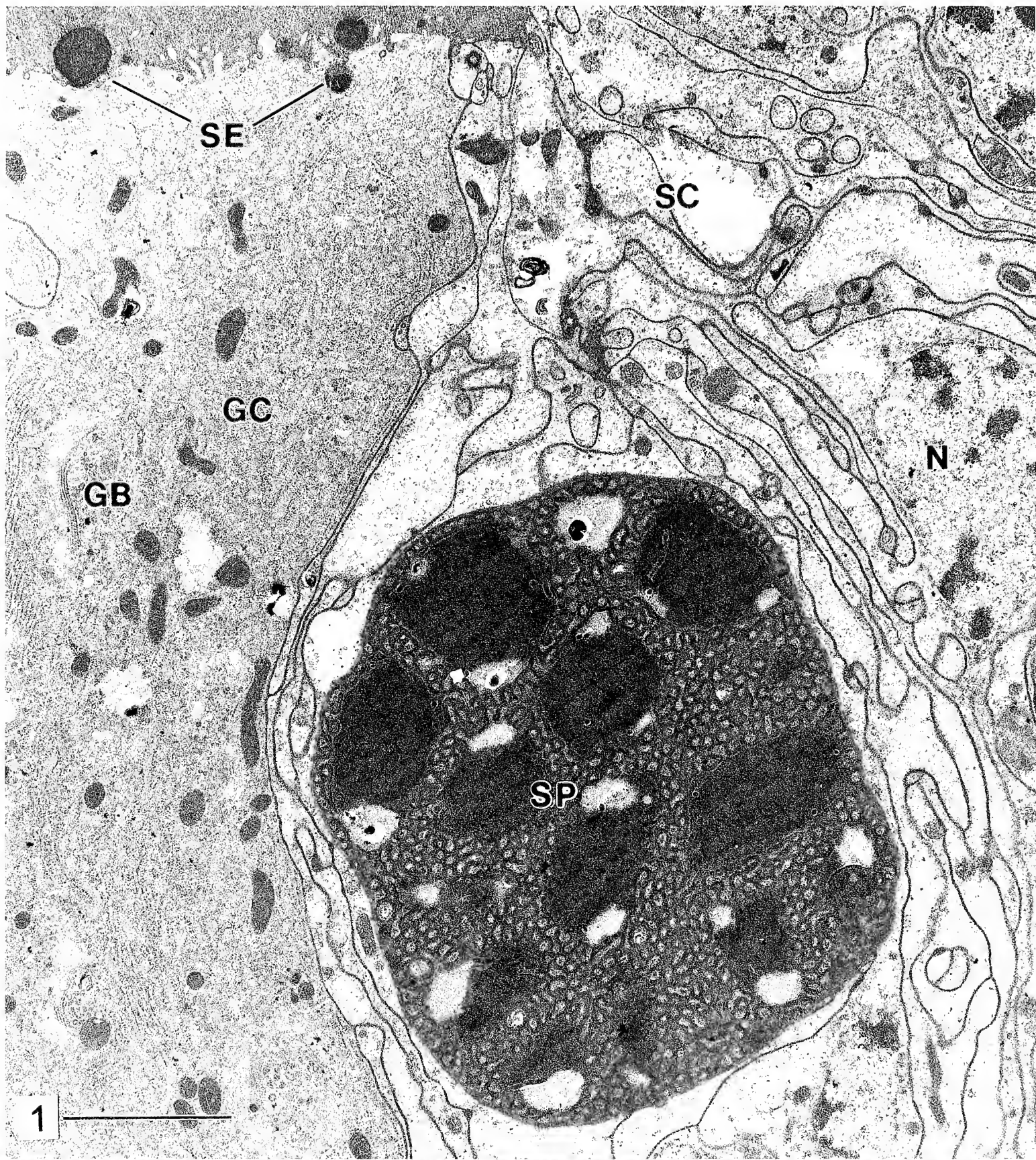
Solifugae present a number of peculiar characteristics that are considered to represent a mixture of plesiomorphies and autapomorphies (Moritz 1993). Hence the position of Solifugae within the Arachnida and their relationship with other taxa is difficult to define. Nevertheless, most authors who have considered the phylogenetic systematics of Arachnida regard Solifugae as most closely related to Pseudoscorpiones (e.g. Weygoldt & Paulus 1979a, b; Hammen 1989; Shultz 1990; Wheeler & Hayashi 1998; Weygoldt 1998). However, this putative sister-group relationship is based on only a few characteristics of debatable value, e.g. rostrum, two-jointed chelicerae and segmentation of the legs (Shultz 1990; Moritz 1993). A relationship between Solifugae and Acari

has frequently been suggested or discussed in the past, but it has never really been accepted (e.g. Hammen 1989; Evans 1992). Hammen (1989), who considered the Acari as being diphyletic, created two taxa Apatellata (Pseudoscorpiones and Solifugae) and Epimerata (Palpigradi and Actinotrichida), which he placed into a sister-group relationship. Dunlop (2000) recently accepted the sister-group relationship between Solifugae and Pseudoscorpiones (forming the Haplocnemata) and suggested Acari as the possible sister group of Haplocnemata.

In general, phylogenetic relationships within the Arachnida are still at least partly controversial. Hence, further characteristics are evidently necessary to improve or falsify suggested concepts. Comparative spermatology

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Figures 1, 2.—Transmission electron micrographs. 1. *Oltacola gomezi* (Solifugae, Ammotrechidae), one group of sperm embedded in germinal layer. At left, glandular tissue. Scale bar = 2 μm . 2. *Oltacola gomezi*, detail of seminal vesicle. Scale bar = 1 μm . Abbreviations: BL = basal lamina, GB = Golgi body, GC = glandular cell, M = mitochondrion, MU = muscle, MV = microvilli, N = nucleus, SC = somatic cells, SD = septate desmosome, SE = secretion, SP = sperm cells.



may provide such characteristics (Jamieson 1987; Alberti 2000).

The only spermatozoa of Solifugae for which the fine structure has been described are those of *Eusimonia mirabilis* Roewer 1934 (Karschiidae) from Morocco (Alberti 1980a). Contrary to descriptions based on light microscopy (Roewer 1934), it was shown that they are highly derivative and differ strikingly from those of Pseudoscorpiones, which present a coiled-flagellate type of sperm and thus are more plesiomorphic (Alberti 1995, 2000). The sperm ultrastructure of *E. mirabilis* shows apomorphic similarities with sperm of actinotrichid mites (Alberti 1980a, b, 2000). The present paper intends to broaden our knowledge of the spermatological characteristics of Solifugae in order to establish whether the results obtained from the single previously investigated species apply more generally to this peculiar order.

METHODS

The following species, both belonging to the family Ammotrechidae, were used for this study: *Procleobis patagonicus* (Holmberg 1876) and *Oltacola gomezi* Roewer 1934. Specimens were captured in San José de las Salinas, Córdoba, Argentina. After dissection, they were fixed in ice-cold 3.5% glutaraldehyde buffered in Sörensen phosphate buffer (pH 7.4; 0.1M). They were then mailed in diluted glutaraldehyde to Germany, where further processing occurred, i.e. postfixation in OsO_4 (2%) and embedding in Araldite. Ultrathin sections were cut with a Leica Ultracut. Transmission electron microscopy was done with Zeiss transmission electron microscopes.

RESULTS

The male reproductive organs of *E. mirabilis*, *O. gomezi* and *P. patagonicus* are rather simple. They comprise a pair of tubular organs starting from a common genital chamber.

A wide seminal vesicle and a pair of long, thin testes is present on each side.

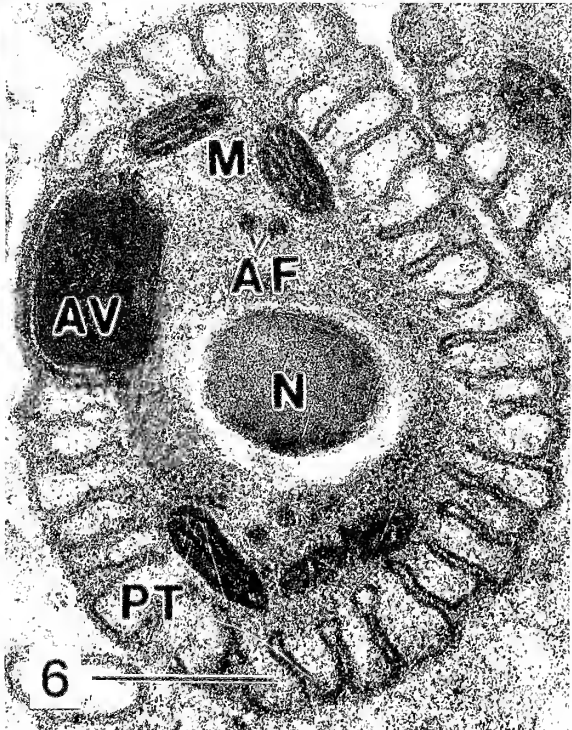
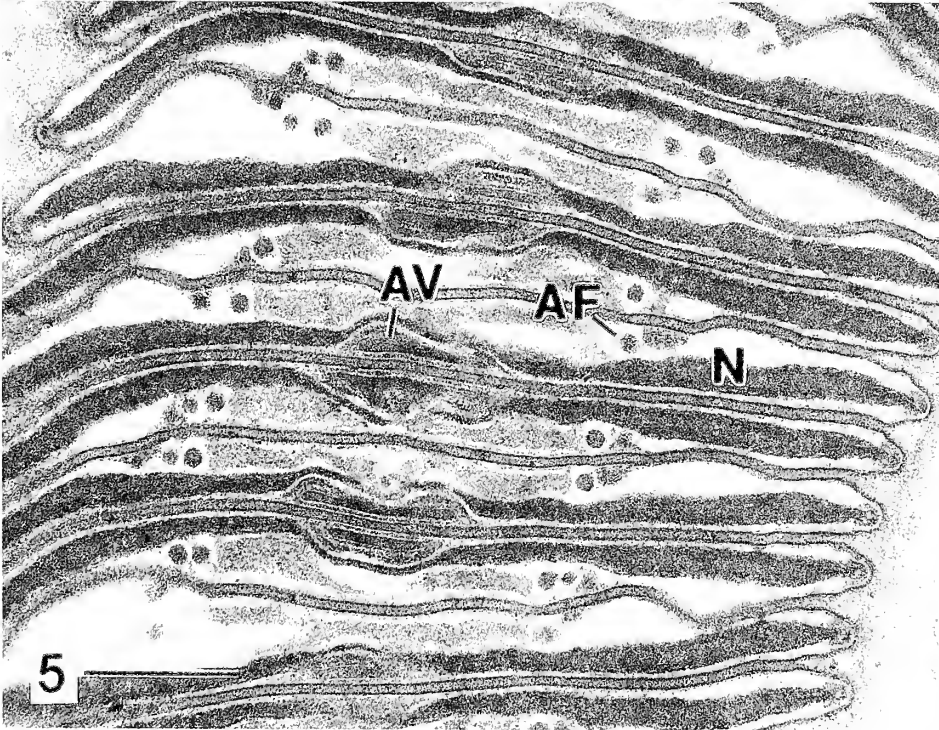
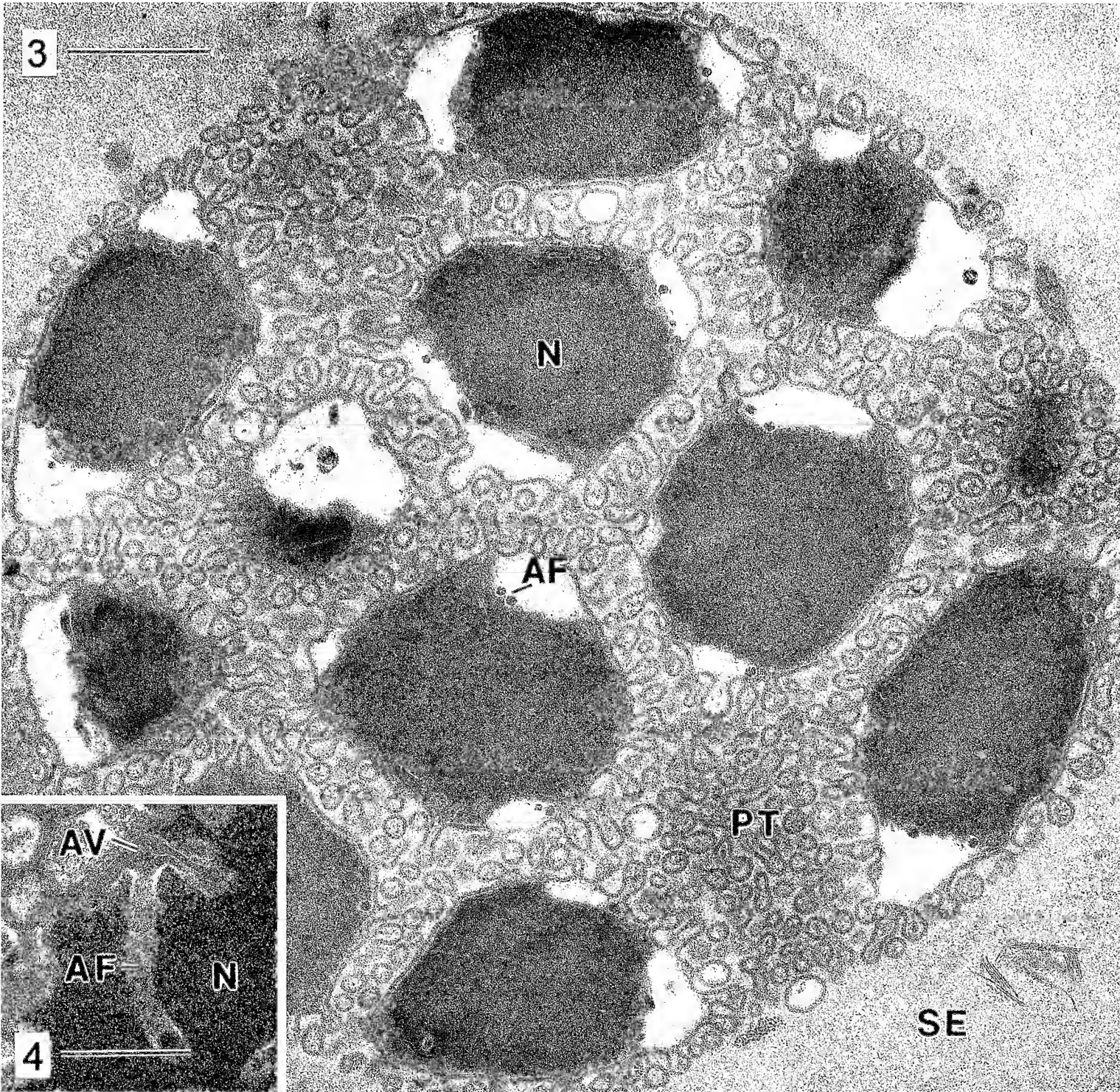
Each testis is composed of a spermatogenic part (germinal layer) and a glandular part that differ strikingly (Fig. 1). The germinal layer comprises somatic cells that form a meshwork in which groups of mature sperm cells are embedded. We did not find earlier stages of spermatogenesis. The larger part of the testis is composed of a glandular epithelium that produces the secretions, predominantly proteinic, found in the narrow testicular lumen and most likely present also in the seminal vesicle.

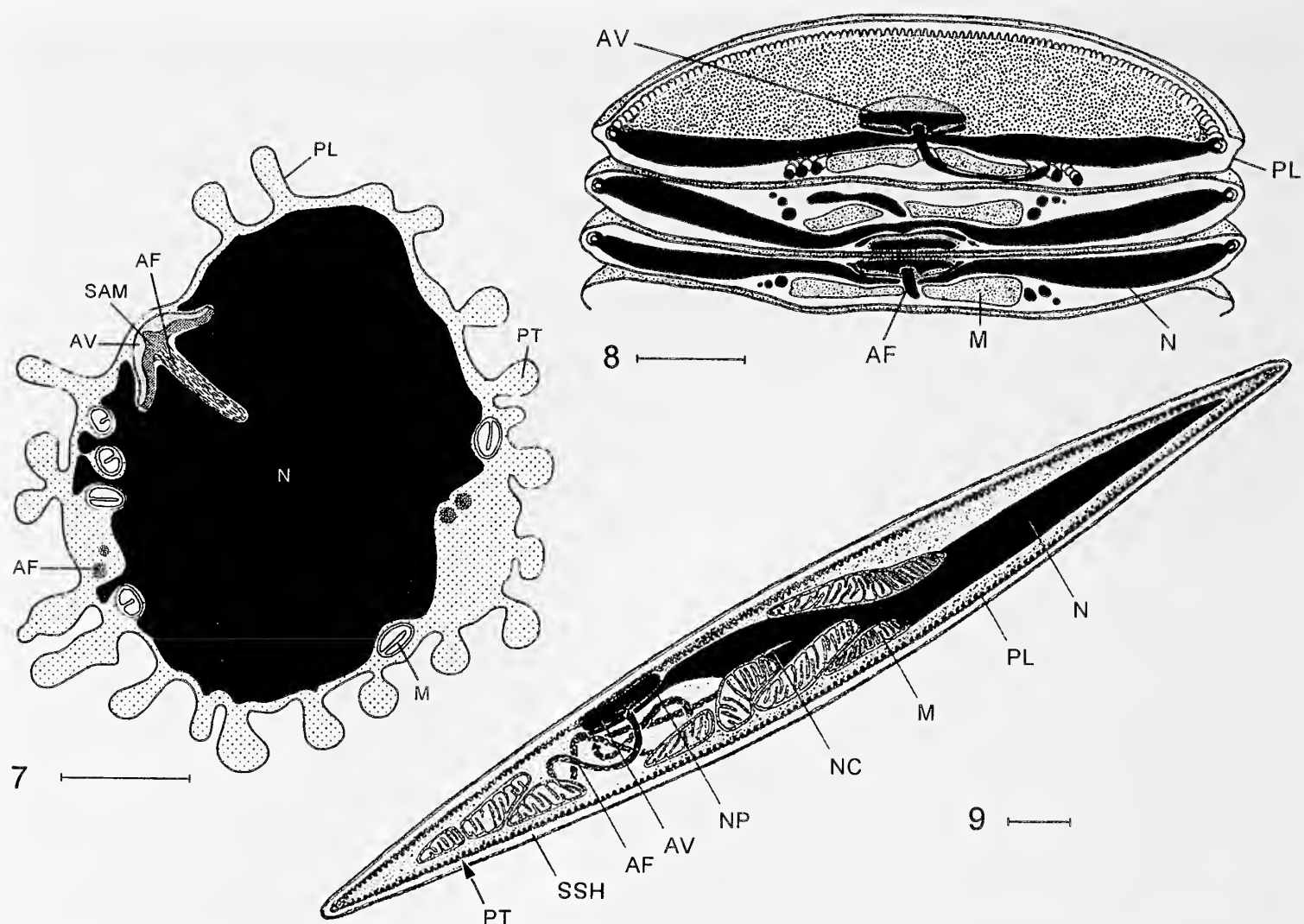
The vesicle wall is composed of a flat epithelium underlain by a few muscle cells (Fig. 2). The wide lumen of the vesicle is filled with secretions and groups of sperm cells. The secretions differ according to the species. In *O. gomezi* there are distinct globules embedded in a homogeneous matrix, whereas such globules are less obvious in *P. patagonicus*. The difference between these secretions may explain an observation during the fixation process: in *P. patagonicus* the tissue in each specimen changed colour, whereas in *O. gomezi* this did not happen.

The groups of sperm cells are highly ordered in *E. mirabilis*, forming piles of regularly arranged sperm cells (Figs. 5, 8). In both the species from Argentina, these groups are less complex. In *O. gomezi*, the spermatozoa collectively form distinct spheres (Fig. 3), whereas in *P. patagonicus* the groups appear less compact. In general, the sperm of all three species investigated are very simple, representing a small (diameter approximately 2 μm) disc- or ovoid-shaped cell devoid of a flagellum (Figs. 3, 7, 8). The cell surface is provided with conspicuous protuberances in the ammotrechid species (Figs. 3, 7), there being less obvious in *E. mirabilis* (Fig. 5, 8). The electron-dense chromatin body (nuclear derivative) is relatively large. It is surrounded

→

Figures 3–6.—Transmission electron micrographs. 3. Spherical sperm aggregate of *Oltacola gomezi*, from vesicle. Note distinct protruberances of plasmalemmae of the sperm cells. Scale bar = 1 μm . 4. *Procleobis patagonicus*, sperm cell from testis showing acrosomal complex. Scale bar = 0.5 μm . 5. Detail of a sperm aggregate of *Eusimonia mirabilis*, from testis lumen. Note regular arrangement of sperm cells. Two discoid sperms form a pair with opposed acrosomal vacuoles. Scale bar = 0.5 μm . 6. Sperm cells from germ layer of testis of *Cyta latirostris* (Actinotrichida, Bdellidae). Scale bar = 0.5 μm . Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, M = mitochondrion, N = nucleus, PT = protuberances, SE = secretion.





Figures 7–9.—Line drawings of sperm cells. 7. *Procleobis patagonicus*. 8. *Eusimonia mirabilis*, detail of a longitudinally sectioned sperm aggregate (from Alberti 1980a). 9. *Bdella septentrionalis* (Actinotrichida, Bdellidae) in longitudinal section (from Alberti & Storch 1976). Scale bars = 0.5 μ m. Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, M = mitochondrion, N = nucleus, NC = nuclear canal, NP = nuclear prolongation, PL = plasmalemma, PT = protuberances, SAM = subacrosomal material, SSH = secretion sheath.

by only a small amount of cytoplasm, containing small mitochondria. A small, flat acrosomal vacuole is located close to the plasmalemma (Figs. 4, 7). The vacuole is underlain by subacrosomal material, from which arises an acrosomal filament (*perforatorium*) that penetrates the chromatin body and finally encircles the chromatin body.

DISCUSSION

Our observations agree with the light microscopic results obtained by Vachon (1945) and Junqua (1966) for species of Galeodidae. Contrary to these authors, Roewer (1934), following Birula (1893–94), also illustrated a number of small accessory glands connected to the genital chamber in *Galeodes araneoides* (Pallas 1772). We have not yet studied this area in our specimens. The fine structure of the male system and spermatozoa of the ammotrechid species is in accordance with that of the karschiid species investigated by Al-

berti (1980a). Hence it is now possible to compare the sperm structure of Solifugae more reliably with that of other arachnid taxa. Earlier statements (Alberti 1980a, b, 1984, 1991, 1995, 2000) that the most similar sperm cells are found within the actinotrichid mites are confirmed (Figs. 6, 9). Sperm cells of representatives of both taxa are small, devoid of a flagellum, contain a chromatin body that is penetrated and surrounded by circles of the acrosomal filament, and have a tendency to form peripheral protuberances. Sperm cells of Anactinotrichida are profoundly different (Alberti 1980b, c, 1984, 1991, 2000; Alberti & Coons 1999). Thus, sperm morphology reflects the remarkable differences that occur also between many other character states of the both major groups of Acari and the question whether Acari represent a monophylum or not has been discussed by several authors (see Lindquist 1984; Hammen 1989; Evans 1992; Alberti & Coons 1999). Because of the

general simplicity of solifugid and actinotrichid sperm cells, we cannot categorically dismiss the possibility that these similarities are the result of convergence. However, the similarity in the fundamental organization of the testis tissue seems to be noteworthy: in both taxa there is a large glandular area that probably produces secretions needed for spermatophore formation. This has not been observed in other arachnids (Alberti 1991, 1995, 2000). Sperm aggregates are also found in certain actinotrichid mites, but may also occur in other arachnid groups (Alberti 1988; Peretti & Batán-Horenstein 2000). Evidently, a close relationship with Pseudoscorpiones, which have coiled-flagellate spermatozoa, is not supported by spermatological results. Except for the peculiar coiling of the flagellate spermatids at the end of spermiogenesis, a process found also in the Megopericulata (Uropygi, Amblypygi, Araneae) and Ricinulei, the sperm cells of Pseudoscorpiones are most similar to those of Scorpiones. Remarkably, the sperm cells of both these latter taxa have strongly modified mitochondria and retain a flagellar tunnel (Alberti 2000). If the similarities between Solifugae and Actinotrichida pointed out here are considered to be result of convergence, one needs to develop a hypothesis about selective forces that could favor evolution of these characteristics. Remarkably, a simple correlation between sperm morphology and sperm transfer, which might be expected, is not yet evident (see Schaller 1979; Weygoldt 1990; Alberti 2000). Alternatively, the assumption of monophyly for Haplocnemata and Acari should be reconsidered.

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THE SUB-SAND NESTS OF *YLLENUS ARENARIUS* (ARANEAE, SALTICIDAE): STRUCTURE, FUNCTION AND CONSTRUCTION BEHAVIOR

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ABSTRACT. An unusual silken nest built under the sand surface is described in *Yllenus arenarius*—a jumping spider inhabiting sandy dunes. In this open habitat, characterized by high temperature and humidity gradients as well as a lack of retreats, the nest probably plays a key role in the survival strategy of *Y. arenarius* that is numerically dominant among day-active, dune-dwelling spiders. These salticids built nests a few millimeters under the surface after burrowing in loose sand. Four types of nests of different size, structure and function were built: A) where eggs were laid and early instars developed, B) where spiders molted, C) where they overwintered and, D) the most common, where spiders spent the night. Different age groups produced different numbers of nests per time unit. Juveniles in their first season of life built many more nests than subadult spiders in their second season, which in turn built more nests than adult spiders. Various functions of the silken nests and the high numbers built by juveniles suggest that the structures may play an important role in surviving in the dune.

Keywords: Salticidae, nest, structure, function, behavior

Yllenus arenarius Menge 1868 is a medium-sized jumping spider with an adult body length of about 6 mm. The spiders inhabit bare areas of sandy dunes primarily in central and eastern Europe (Prószyński 1991; Żabka 1997), tending to keep away from dense vegetation. They are numerically dominant among day-active arachnids. Their life span in the field reaches about 700 days. The spiders hatch in spring and die two years later, overwintering twice (as juveniles and as adults). Thus, in the field, two cohorts can be found simultaneously (Bartos 2000).

Much attention has been paid to spider webs (e.g., Shear 1986; Foelix 1996). Studies on various aspects of webs resulted in our knowledge of the web architecture and web-building behavior of numerous spiders (e.g., Zschokke & Vollrath 1995), as well as the physical and chemical properties of certain web elements (e.g., Peters 1987; Tillinghast & Townley 1987). However, surprisingly little is known about the cocoons and nests. They are all also silken products, possessing distinct structures and properties (Hieber 1985; Nentwig & Heimer 1987; Hieber 1992a,b). Nests are crucial for the spiders' development. They provide stable temperature and humidity con-

ditions for eggs as well as for hatching and molting spiders (Nentwig & Heimer 1987). In the stages when spiders cannot defend themselves against predators, nests also provide safe retreats (Foelix 1996).

Relatively more attention has been paid to the nests of jumping spiders, which are both variable and specialized (Jackson 1985; Hallas & Jackson 1986; Jackson 1989). From these and other studies we know that, apart from the typical functions, nests produced by certain jumping spiders also play an important role in species recognition, courtship, and mating (Jackson 1981, 1982a, b, 1983, 1986). Some of the nests have prey-holding abilities and may play a role in prey capture (Hallas & Jackson 1986). In this paper, the structure, function and building behavior as well as the age-dependent differences in nest building by *Y. arenarius* will be considered.

METHODS

Data were taken in the field as well as in the laboratory. Adult and juvenile individuals of *Yllenus arenarius* were collected from 14 sites in central and eastern Poland. From one of the sites (Kwilno) in central Poland they were collected regularly—every two weeks.

Four measurements were taken of live specimens with a stereomicroscope (precision, 0.1 mm): body length (BL), abdomen length (AL), abdomen width (AW) and posterior eye width (PEW). The sex and age of the spiders were also recorded.

Spiders were kept individually in glass containers (1 liter) with a 3 centimeter-thick layer of dune sand on the bottom. Temperature was ca. 25 °C, light regime 12L: 12D, and the sand was moistened weekly with 5 ml of water. Spiders were fed *ad libitum* (10 fruit flies twice a week). Under these conditions 90 spiders were reared and their nests were collected.

Sand from lab containers was sieved every two weeks in order to collect nests. Nest length (NL) as well as nest width (NW) were measured (precision, 0.1 mm). The measurements were taken from adults or, in the cases of nests used for molting, from subadult spiders. To describe the ratio of nest length (NL) to spider body length (BL), NL/BL was calculated. The ratio of nest width (NW) to spider abdomen width (AW), was given as NW/AW. The nests were opened and checked for eggs and exuvia and to assess nest wall transparency. The wall transparency was assigned to one of three categories according to Jackson (1979): 1—transparent silk; 2—nearly opaque; 3—completely opaque (sand grains were invisible through the silk).

In winter a two centimeter thick layer of sand was collected from the dune surface. Sand was dried in the lab (temperature ca. 25 °C). Spiders active on the sand surface were collected, measured and reared. Dried sand was sieved in order to collect nests and immersed spiders. Burrowing was recorded with a camera and the nest building behavior was analyzed on the basis of observations taken at certain stages of the process, which was interrupted by blowing the sand off the spider during nest building.

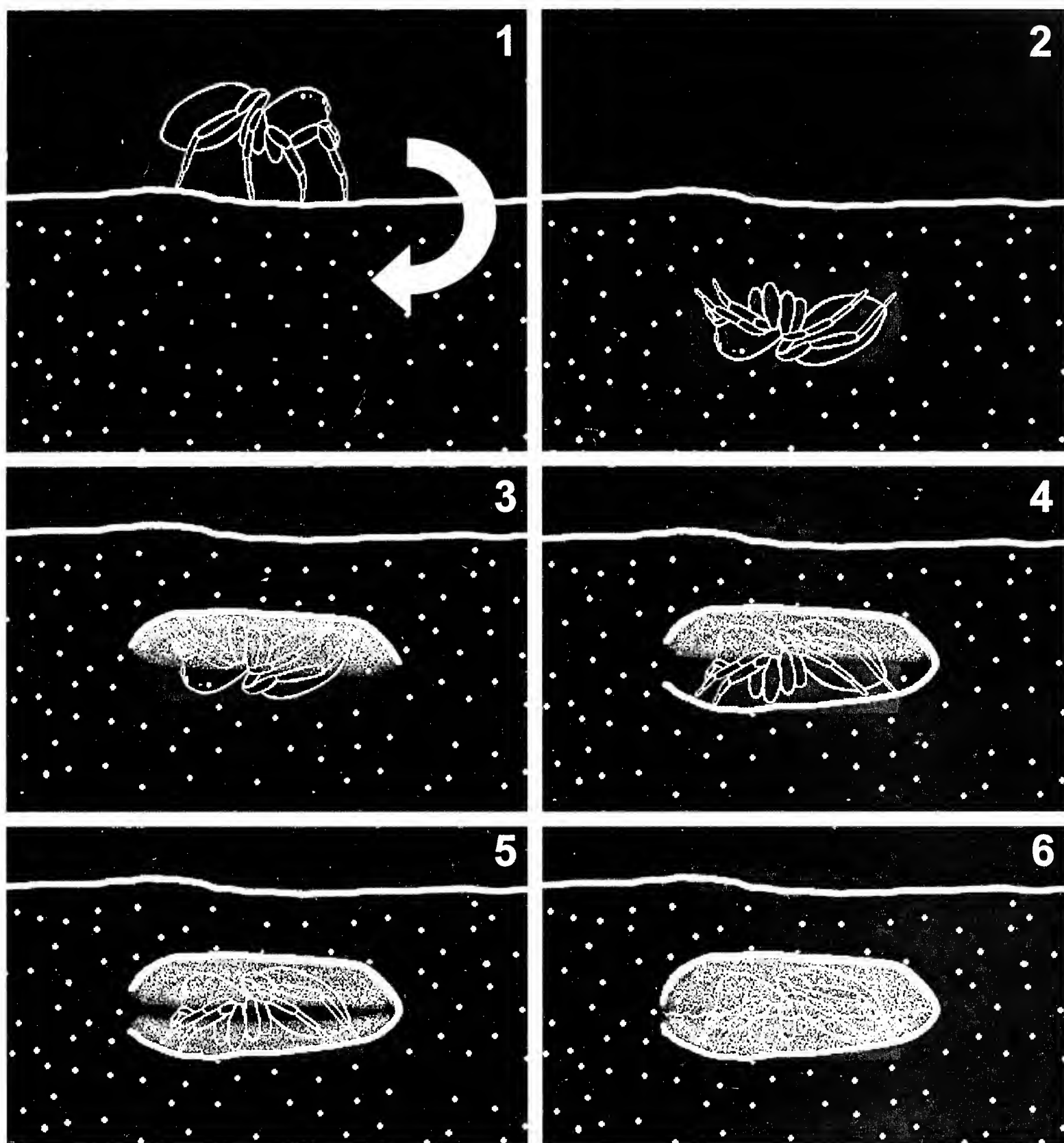
All statistical procedures followed those described by Zar (1984). Comparisons between relative length (NL/BL) and width (NW/AW) of different nest types and the number of nests produced daily were conducted using the Kruskal-Wallis test (H), followed post-hoc by nonparametric Tukey-type multiple comparisons (Q). Data are presented as mean \pm SD (*n*).

RESULTS

Yllenus arenarius was found to build nests under the sand surface (ca. 5 mm under the surface). Before starting to construct a nest spiders dug themselves into the sand (Fig. 1). The spiders immersed themselves in the sand without excavating. They used legs I to scarify and dive into the sand. Legs II were used to push the sand aside, which allowed the spider to pull into the sand. The process of diving took an average of 81.6 ± 43.1 sec. (*n* = 10). A spider immersed in the sand lay upside down and began to build the top wall (the “ceiling”) of the nest (Figs. 2, 3). The sheet of silk was spun and spread aside with the legs. The next stages could not be observed, however the structure of the nest and the spider’s position in the last observed stage suggested that the spider then turned rightside up and spun the bottom wall (the “floor”) of the nest (Figs. 4, 5). Finally both walls were bound together with silk (Fig. 6). This scenario seems reasonable since the nest is made of two thick layers of silk, which are difficult to tear apart. The nest, however, can easily be torn into two pieces along the lateral line, which binds the two walls.

The nest of *Y. arenarius*, as viewed from above, is an oval, pear-shaped or rectangular sac with sand and organic matter glued in the silk. Nests usually had one main opening, which could elastically expand when the spider was leaving the chamber. Sometimes another small aperture was found on the opposite end of the nest. Because of its small diameter (too small for a spider to get through and never used in escape), it was probably an unwoven hole rather than a second opening. Silk inside the nest was probably non-adhesive because sand did not tend to stick to it. The outer layer of silk, however, was adhesive since sand grains stuck to it firmly.

Nests built for various purposes differed in size, structure and wall transparency. The function of different nest types appears obvious when analyzing the nest content, time of the day and season when built. On those bases, the following four nest types were distinguished. Type A (nests where eggs are laid and young spiders develop) were oval or slightly elongated sacs (Table 1). Layers of silk and sand made the walls slightly rigid and convex (wall transparency, 2). The nests con-



Figures 1–6.—Burrowing and nest building in *Yllenus arenarius*. 1. Spider on the sand surface. 2. Immersed spider in upside down position. 3. Building top wall of nest. 4. Spider after turning rightside up. 5. Building bottom wall of the nest. 6. Binding top and bottom walls together.

tained on average 6 ± 0.8 eggs ($n = 5$). Chorion sheaths and juvenile exuvia were also found there. Two thin, inner walls made of silk were unique for this nest type. One of them covered the eggs so that they were held against the bottom of the nest. The other wall was a vertical one placed close to the entrance separating it from the main chamber containing the eggs. The latter silken layer was made by the female probably after she had laid the

eggs. In the lab, these nests were only found in the spring. Type B (nests where spiders molt) were oval or elongated, convex sacs made of several layers of silk and sand (Table 1) (wall transparency, 2). Exuvia were found only in this type of nest. Type C (nests where spiders overwinter) were densely impregnated with organic matter and the most elongated of all nests—almost tubular (Table 1). The nests were convex and had the thickest walls of all

Table 1 The four nest types of *Y. arenarius* and their measured properties. (NL: nest length, NW: nest width, BL: body length, AW: abdomen width).

Nest type	NL (mm) mean±SD (n)	NW (mm) mean±SD (n)	NL/BL mean±SD (n)	NW/AW mean±SD (n)
A: where eggs and young spiders develop	13.44 ± 1.70 (5)	9.53 ± 1.16 (5)	1.98 ± 0.25 (5)	3.74 ± 0.45 (5)
B: where spiders molt	13.96 ± 3.15 (8)	8.34 ± 1.29 (8)	2.62 ± 0.37 (8)	3.71 ± 1.02 (8)
C: where spiders overwinter	16.12 ± 1.13 (3)	8.89 ± 0.87 (3)	2.42 ± 0.33 (3)	3.21 ± 0.46 (3)
D: where spiders spend the night	8.22 ± 0.74 (6)	6.89 ± 0.52 (5)	1.81 ± 0.74 (32)	3.47 ± 0.58 (32)

types (wall transparency, 3). They were found only in winter sand samples. Type D (nests where spiders spend the night) were round, oval or rectangular with flat walls. They were the most fragile of all nests, with thinnest walls (wall transparency, 1). These nests were produced more often than other types (up to 1 each 24h). Nests collected from the same sample (built by the same individual) varied in size (Table 1). The last nest built (where the spider was found during sieving) was not usually the largest one. Comparison of relative nest length (NL/BL) of all types of nests revealed that type D nests were significantly shorter than type B nests ($Q = 4.54$; $df = 4$; $P < 0.05$) and type C nests ($Q = 2.81$; $df = 4$; $P < 0.05$). The differences in relative nest width (NW/AW) between all types of nests were not significant ($H = 1.21$; $df = 3$; $P > 0.75$).

Spiders in successive age groups built respectively larger nests. Early instars started to build overnight nests soon after leaving the nest, where they hatched (type A). These nests were rectangular and had very thin walls. Nests of later stages were bigger, generally more oval and had thicker walls.

Juvenile spiders in the first and at the beginning of the second year of life built on average 0.94 ± 0.55 nests/day ($n = 129$), which is 18.8 times more than in subadults (0.05 ± 0.12 nests/day, $n = 39$). The difference is significant ($Q = 8.27$; $df = 3$; $P < 0.05$). Juvenile spiders built 31.3 times more nests than adult spiders (0.03 ± 0.06 nests/day; $n = 18$). The difference is also significant ($Q = 6.13$; $df = 3$; $P < 0.05$). The differences between subadult and adult spiders in the number of

nest built daily were not significant ($Q = 0.39$; $df = 3$; $P > 0.05$). Adult spiders were often found immersed in sand but with no nest.

DISCUSSION

Nests built by *Y. arenarius* under the sand surface are an interesting and unique adaptation to survival in dunes. In the sandy habitat characterized by high daily and seasonal temperature and humidity gradients as well as lack of retreats, underground nests provide shelter against night-active predators, strong wind and periods of inclement weather such as heavy rains. Water from rain floods river-side and marine dunes, temporarily inundating the habitat, and may be a severe mortality factor. The waterproof properties of silken walls and their permeability to air, which allows functioning as a physical gill (Hieber 1985, 1992a; Nentwig & Heimer 1987), may significantly reduce the spider's mortality under conditions of flooding. This, however, has not been studied in *Y. arenarius* and requires further research.

Differences in wall transparency (wall thickness) of nests of jumping spiders have already been reported. Jackson (1979) describing variations in the nests of *Phidippus johnsoni* (Peckham & Peckham, 1883) mentioned that nests where molting and oviposition took place were made of dense silk. This study confirmed that observation. The lower wall transparency (the higher wall thickness) in these kinds of nests is probably related to the high susceptibility of eggs and spiders during molting to changes in humidity (Hieber 1992a). The differences in wall thickness re-

sult in its rigidity and may therefore influence the shape of the nest.

Jumping spiders differ as to whether they return to previously built nests. A study by Jackson (1979) of *P. johnsoni* revealed that the spiders employ the same nest for prolonged periods, while lack of homing behavior was found in *Salticus scenicus* (Clerck 1757) (Plett 1962). In case of *Y. arenarius* there are several observations strongly supporting the idea that the spiders do not use their nests repeatedly. Juveniles build a new nest on average every day and later instars were usually found with more than one nest in the lab sand sample. After leaving a nest, a little pit, indicating where the spider emerged onto the surface is very quickly filled with wind blown sand. Nests are built in areas of almost bare sand with very few structures allowing landmark orientation. The wandering spider is unlikely to be able to recognize or localize the nest site when it has emerged from its underground nest. Furthermore, a spider returning to the nest would bring in some grains of sand, which were never found in the nests.

The importance of the nests where spiders molt, lay eggs and overwinter is not in doubt. These functions were never recorded outside the nests. The function of the overnight nests is much less clear. Adult spiders were found spending the night in the sand without the nest, so the nest does not appear to be crucial for their survival. If adult spiders were found to build few overnight nests but juveniles found to build many, one could conclude that the nest plays a more important role for juveniles. It is possible that the difference in the number of nests produced at different ages is related to a higher susceptibility to humidity changes in juvenile spiders especially during molting (Hieber 1992a). In adult spiders the costs connected with silk production and nest building may be higher than the advantages of using a nest. The surface to volume ratio is lower in the case of an adult's nests than in a juvenile's nests (which implies that the latter should use relatively more silk). The silk threads, however, produced by juveniles are thinner and the layers of silk building the nest walls may be fewer, suggested by the higher rate of damaged nests.

This study is the first attempt to describe and understand the variability of nests and unusual nest building behavior in *Y. arenarius*.

Further studies to determine nest function are clearly needed.

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THE PLACEMENT OF *PERILLA* (ARANEAE, ARANEIDAE) WITH COMMENTS ON ARANEID PHYLOGENY

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ABSTRACT. The Oriental spider genus *Perilla* Thorell is revised, diagnosed and transferred from the tetragnathid subfamily Nephilinae to the araneid subfamily Araneinae. Cladistic analysis of recently published araneid matrices with the addition of *Perilla* supports this new placement. *Perilla* groups with *Chorizopes* O. P.-Cambridge, previously a basal araneid. *Perilla teres* Thorell, the type species of the genus, is redescribed. The only other known species, *Perilla cylindrogaster* Simon, is proposed as a junior synonym of *P. teres*, which renders *Perilla* monotypic.

Keywords: Araneidae, Araneinae, Nephilinae, Tetragnathidae, cladistics, spiders, *Perilla*, *Chorizopes*

The history of the tetragnathid subfamily Nephilinae was most recently reviewed by Hormiga et al. (1995). Tetragnathidae currently contains seven nephiline genera (Platnick 1997, 2001): *Nephila* Leach 1815, *Clitaetra* Simon 1888, *Deliochus* Simon 1894, *Herennia* Thorell 1877, *Nephilengys* L. Koch 1872, *Perilla* Thorell 1895, and *Phonognatha* Simon 1894. Kuntner & Hormiga (in press) recently transferred *Singafrotypa* Benoit 1962 to Araneidae.

While Hormiga et al. (1995) established the monophyly of Nephilinae containing the genera *Phonognatha*, *Clitaetra*, *Nephila*, *Nephilengys* and *Herennia*, the systematic placement of *Deliochus* (from Australia) and *Perilla* (from Myanmar and Vietnam) has remained doubtful. These two genera have not been redescribed since their first descriptions in the 19th century. In this paper I redescribe the genus *Perilla* and incorporate it into a cladistic analysis to test its familial placement. The results imply that *Perilla* is an araneid, not a tetragnathid.

Taxonomic history.—Thorell (1895) erected monotypic *Perilla* and described *P. teres* Thorell 1895 from Burma (today Myanmar). Thorell placed the genus in the family Euetrioidae (today Araneidae). Simon (1909) described the second species, *P. cylindrogaster* Simon 1909 from Vietnam, and listed *Perilla* within his argiopid subfamily Argiopinae close to *Araneus*, and not in his argiopid sub-

family Nephilinae. While Bonnet (1958) lists *Perilla* in Argiopidae, Roewer's (1942) judgment was that *Perilla* belongs to the araneid subfamily Nephilinae. It has remained there since (Brignoli 1983), but the subfamily recently changed its familial assignment (see Hormiga et al. 1995). Consequently, in all Platnick's catalogues (1989, 1993, 1997, 2001) *Perilla* is a tetragnathid.

METHODS

Morphology.—General methods of study are described in Hormiga (1994). All morphological observations and illustrations were made using a Leica MZ APO dissecting microscope. Illustrations were made using a camera lucida and rendered on coquille board. Measurements were taken using a reticle and are in millimeters. Abbreviations of the specimen depositories are NHM (The Natural History Museum, London), MNHN (Muséum National d'Histoire Naturelle, Paris), and CD (Christa Deeleman-Reinhold's private collection, Ossendrecht, The Netherlands).

Phylogenetic analysis.—Examination of the syntype male of *Perilla teres* allows homologizing most palpal sclerites and some general somatic traits with those of araneids (see Taxonomy). *Perilla teres* lacks the three synapomorphies currently hypothesized to support tetragnathid monophyly (Hormiga et al. 1995): absence (loss) of median apophysis, embolus and conductor spiraling with each

other, and apical tegular sclerites. To phylogenetically test the placement of *Perilla* within Araneidae, I used the published data of Scharff & Coddington (1997), containing 57 araneid genera plus 13 genera from eight outgroup families scored for 82 morphological and behavioral characters. The outgroup taxa include the true nephiline genera *Nephila* and *Nephilengys*. In addition, I used Kuntner & Hormiga's (in press) codings for *Singafrotypa acanthopus* (Simon 1907) and *Singafrotypa okavango* Kuntner & Hormiga (in press). To these data I added new coding for *Perilla teres*: 00011100000000011??101010000---0000000111000100011100000-00000000001002?010???????

Thus the matrix analyzed here had a total of 73 taxa scored for 82 characters. Since only the syntype male of *P. teres* was available for my examination, I refrained from expanding its palps. This made it impossible to determine the presence of some palpal sclerites, such as stipes and paramedian apophysis (for interpretation of other morphological characters see species description below). For female morphology I used both examined females (see below). I was able to score some of the behavioral characters of Scharff & Coddington (1997) for *Perilla* by using field notes of Dee-leman-Reinhold (in litt.) and from the information from Murphy & Murphy (2000). I coded all ambiguities in the matrix as unknown entries.

The parsimony analyses were performed using the computer programs PAUP* version 4.0b4a (Swofford 2000) and NONA version 2.0 (Goloboff 1993). In PAUP I used random taxon addition for 10 replicates and TBR branch swapping. In NONA I used search parameters 'hold 10000', 'mult*500', 'max*', and 'sswap', under both 'amb -' and 'amb ='. Winclada version 0.9.99m24 (Nixon 2000) was used to display and manipulate trees and matrices for NONA. The 14 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971).

RESULTS AND DISCUSSION

The parsimony heuristic searches in PAUP* and NONA combined produced 2750 trees of minimal length (291 steps) with consistency and retention indices of 0.34 and 0.74, respectively. All the minimal length topologies

have in common the placement of *Perilla* within the araneid subfamily Araneinae, as well as the monophyly of Araneidae and Tetragnathidae. These results are grossly congruent with those of Scharff & Coddington (1997) (but see below), and with the results of Kuntner & Hormiga (in press) in the placement of *Singafrotypa* within Araneinae.

In the strict consensus cladogram of the 2750 trees most resolution within Araneinae is lost compared to the preferred cladogram of Scharff & Coddington (1997). This is not surprising, since they defended one of the most parsimonious trees and argued that strict consensus obscured the phylogenetic signal they found (Scharff & Coddington 1997: 403): "We also found it useful to avoid the use of strict consensus trees. The solution set of 16 most parsimonious trees presents nearly a 'bush' among araneines if a strict consensus tree is computed."

Perilla and *Chorizopes* O.P.-Cambridge 1870, two genera previously not araneines, form a clade in the strict consensus cladogram. *Perilla* has never been subject to phylogenetic analyses, and *Chorizopes* has been a basal araneid in the preferred tree of Scharff & Coddington (1997), although the authors wrote (p. 423) that such a result is controversial, and that the genus probably belongs among basal araneines, as found here. The synapomorphies (unambiguous optimization) for the clade (*Perilla* + *Chorizopes*), though homoplasious in this analysis, are the characters and states 41(1), 50(1) and 64(0) of Scharff & Coddington (1997): glabrous female carapace, wide separation of lateral and median eyes, and normal (not grooved) female booklung cover, respectively.

In my current analysis, all most parsimonious trees support Kuntner & Hormiga's (in press) transfer of *Singafrotypa* from Nephilinae (Tetragnathidae) to Araneinae (Araneidae), and its placement as sister to the clade *Araniella* (*Alpaida* (*Enacrosoma* + *Bertrana*)), as previously hypothesized by Kuntner & Hormiga (in press).

How robust are the results of the current analysis? The clade (*Perilla* + *Chorizopes*) survives at least one round of Bremer support, although tree buffers were filled with 32,750 trees long before all trees of the length 292 were found. However, the many disagreements between my results and those of Scharff

& Coddington (1997) suggest that the phylogeny of Araneinae is still very much an open question. It is likely, therefore, that the sister group relation between *Perilla* and *Chorizopes* may be refuted in the future, or that the current phylogenetic structure of Araneinae may be seriously altered. For a reliable placement of *Chorizopes* one would have to score the type species, *C. frontalis* O.P.-Cambridge from Sri Lanka. Scharff & Coddington (1997) scored an unidentified species of *Chorizopes* from Madagascar. Furthermore, the placement of *Perilla* should be rigorously retested when more material allowing dissection becomes available. My current hypothesis, thus, should not be taken as a new proposal of araneid phylogeny but rather as a phylogenetic test corroborating the araneine placement of *Perilla*.

TAXONOMY

Perilla Thorell 1895

Perilla Thorell 1895: 195–196; Roewer 1942: 934; Bonnet 1958: 3484; Brignoli 1983: 241; Platnick 1989: 299; Platnick 1993: 371; Platnick 1997: 452. Type species, by original designation, *Perilla teres* Thorell 1895.

Etymology.—Thorell (1895: 195) named the genus after *Perillus* with no further explanation. Supposedly, this refers to the designer of a bronze bull in which *Phalaris*, the tyrant of Agragas (modern Agrigento in Sicily) has roasted his victims alive, their shrieks representing the animal's bellowing (*Encyclopaedia Britannica Online*: www.eb.com). *Perillus* was said to have been the first man executed in the bull.

Diagnosis.—*Perilla* is diagnosed by its extremely elongated cylindrical abdomen, which extends far beyond the spinnerets in both sexes, but especially in females (Fig. 1). The ratio of the posterior part of abdomen (beyond spinnerets) to abdomen length in females is 0.53. This is much greater than in other araneid genera, in which the abdomen extends beyond the spinnerets: 0.29 in *Acusilas* Simon 1895 (measured in *A. coccineus* Simon 1895), 0.25 in *Hingstepeira* Levi 1995 (calculated for *H. folisecens* (Hingston 1932) from Levi 1995), 0.23 in *Cyclosa* Menge 1866 (calculated for *C. conica* (Pallas 1772) from Levi 1999), 0.21 in *Singafrotypa* (measured in *S. acanthopus*), 0.20 in *Milonia* Thorell 1890 (measured in *M. trifasciata* Thorell 1890). All these genera

lack the thicker first two pairs of legs present in *Perilla*. *Perilla* further differs from *Singafrotypa* by lacking an epigynal scape, and by having a narrow eye region of the prosoma. A unique combination of male sexual characters are the pointed paracymbium (Fig. 6) and a pointed ending of the tegulum (Figs. 5, 6).

Natural history.—Christa Deeleman-Reinhold (in litt.) observed *Perilla teres* in Genting Highlands, Malaysia (see material examined). The spiders were found in open country, at the top of grass stems of approximately 1 m. The grass stem top is bent by the spider and folded into an elongated tubular retreat, glued with silk over the full length. The spider preys within the retreat and is connected to the hub of its asymmetric orb web via signal thread. Murphy & Murphy (2000) provide the only published information on *Perilla* biology (almost identical to the above information) with photographs of a female and her web. These were also taken at Genting, and thus are likely to depict *Perilla teres*.

Composition.—*Perilla cylindrogaster* Simon 1909 is proposed as a junior synonym of *Perilla teres* Thorell (see below), which renders *Perilla* monotypic.

Perilla teres Thorell 1895

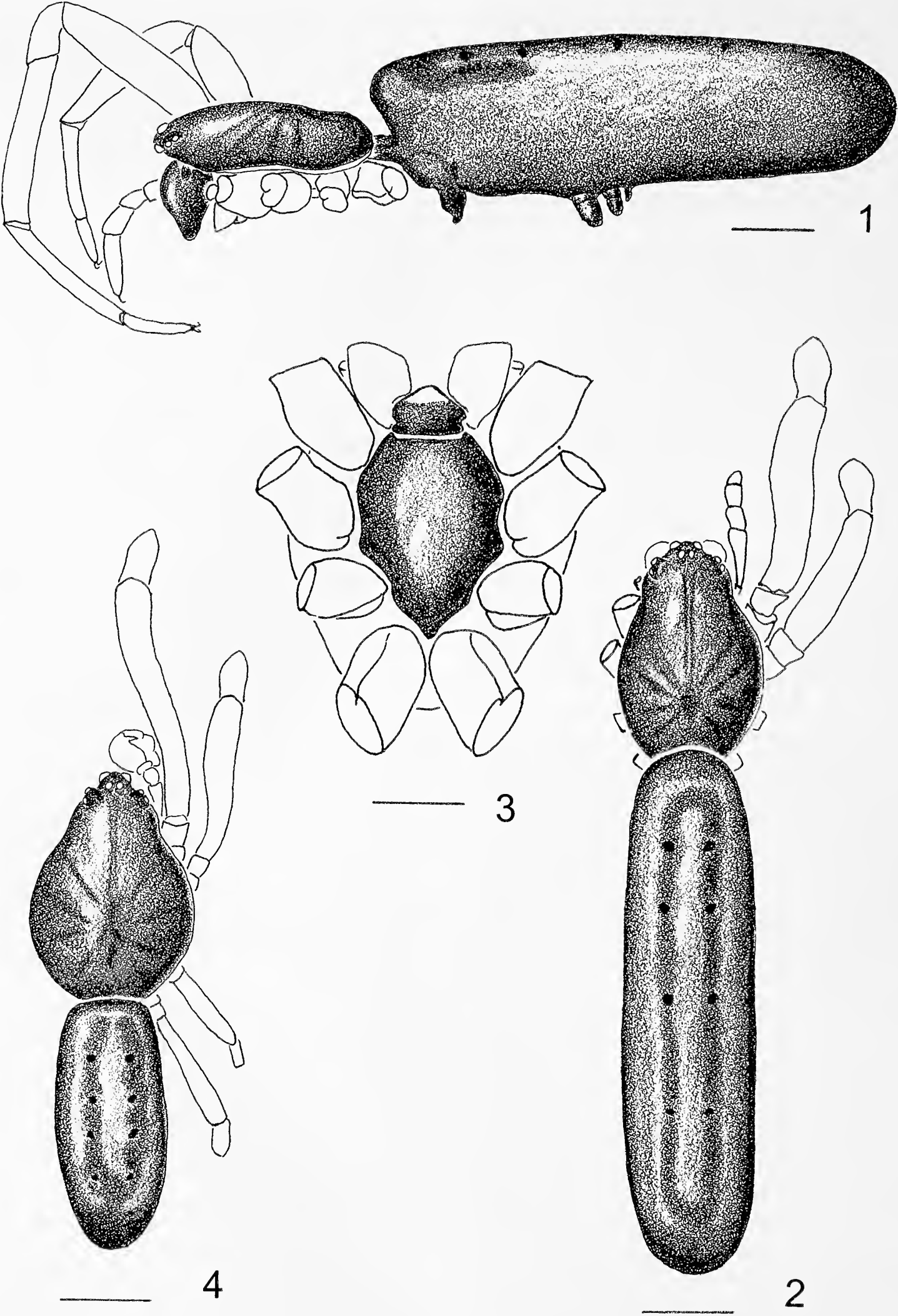
Figs. 1–9

Perilla teres Thorell 1895: 196–199, description of male, female. Roewer 1942: 934. Bonnet 1958: 3484.

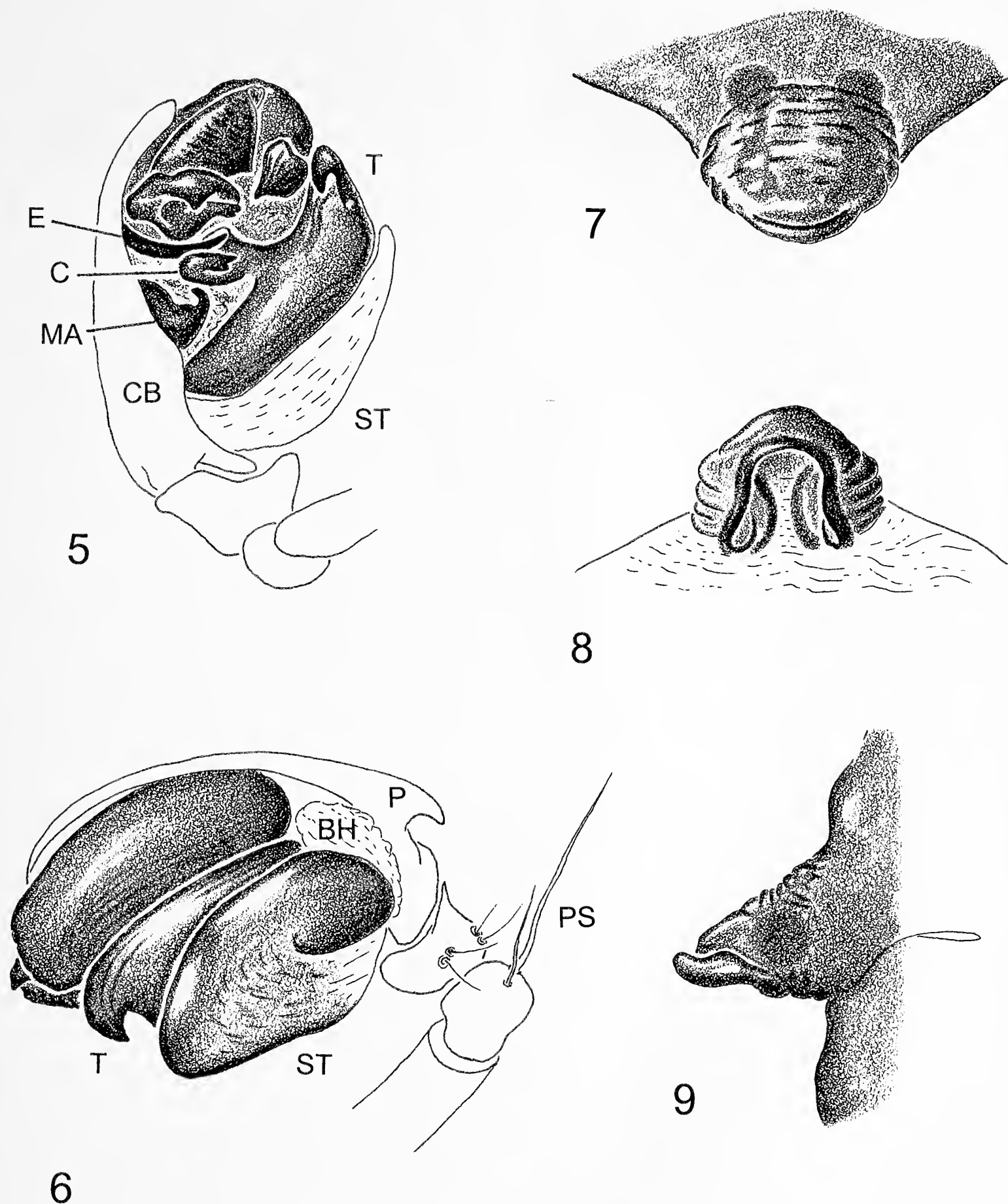
Perilla cylindrogaster Simon 1909: 110–111, description of female. Roewer 1942: 934. NEW SYNONYMY.

Types.—Thorell's syntype male and female of *Perilla teres* from Tharrawaddy, Myanmar, in NHM, examined. The holotype of *Perilla cylindrogaster* from Tonkin, Vietnam, in MNHN, was examined, and is immature. See Note below for justification of synonymy of *P. cylindrogaster* with *P. teres*.

Description.—*Male* (syntype): Figs. 4–6: Total length 5.27. Cephalothorax 2.64 long, 1.9 wide, 0.77 high. Sternum 1.11 long, 0.77 wide. Abdomen 2.79 long, 1.25 wide. Femur I length 2.73, Patella I length 0.78, Tibia I length 2.33, Femur IV length 1.40, Patella IV length 0.63, Tibia IV length 1.48. Chelicerae with 5 prolateral and 3 retrolateral teeth, and approximately 14 denticles in between. Prosoma red-brown, sternum brown with dark



Figures 1-4.—*Perilla teres* Thorell. 1-3. Female syntype from Tharrawaddy, Myanmar; 1. Lateral; 2. Dorsal; 3. Sternum and labium; 4. Male syntype from Tharrawaddy, Myanmar, dorsal. Scale bars = 1.0 mm, except in Fig. 3 = 0.5 mm.



Figures 5-9.—*Perilla teres* Thorell. 5-6. Left male palpus (syntype); 5. Mesal; 6. Ectal; 7-9. Epigynum (syntype); 7. Frontal; 8. Caudal; 9. Lateral. Scale bar = 0.5 mm. Abbreviations: BH = basal hematodocha; C = conductor; CB = cymbium; E = embolus; MA = median apophysis; P = paracymbium; PS = palpal patellar setae; ST = subtegulum; T = tegulum.

gray patches, chelicerae red-brown. Endite with a lateral tooth. Legs yellow and distally somewhat darker, the longer first two pairs thicker and longer. Coxae and tibiae not modified. Abdomen gray with a darker patch on posterior dorsum (Fig. 4) and on venter. Pedipalp as in Figs. 5, 6. Palpal femur without tubercle, two macrosetae of subequal size present on the palpal patella (Fig. 6). Paracymbium pointed (Fig. 6) and the tegulum has a pointed ending (Figs. 5, 6). Median apophysis pointed (Fig. 5), conductor accommodates the embolus tip, which is simple, without a cap. Sclerites of the embolic division remain unidentified (Fig. 5) because expanding of the palp is necessary to homologize them. Radix was observed through the cymbium, and some of the unidentified distal sclerites (Fig. 5) are hypothesized to be the terminal and subterminal apophyses. Consequently, presence of the distal hematodocha is postulated, though not observed. Unobserved, if present, remain the stipes and the paramedian apophysis.

Female (syntype): Figs. 1–3, 7–9: Total length 8.06. Cephalothorax 2.5 long, 1.64 wide, 0.63 high. Sternum 1.1 long, 0.78 wide. Abdomen 5.7 long, 1.72 wide. Femur I length 2.38, Patella I length 0.85, Tibia I length 2.0, Femur IV length 1.34, Patella IV length 0.70, Tibia IV length 1.44. Chelicerae with 4 prolateral and 3 retrolateral teeth, and approximately 12 denticles in between. Prosoma red-brown, sternum dark brown laterally and yellow in the middle (Fig. 3), chelicerae red-brown. Legs yellow, the longer first two pairs thicker and annulated dark brown. Abdomen gray with darker patches on anterior and posterior dorsum (Fig. 2) and ventrally between epigynum and spinnerets. Epigynum a protruding sclerotized plate (Figs. 7–9).

Variation.—The female and subadult male of *P. teres* from Malaysia (locality data below) are darker than the syntypes, with a dark brown prosoma and legs, uniformly dark brown sternum, and dark gray abdomen. The female leg macrosetae are more numerous than in the syntype. The epigynum of this female was not protruding and had to be dissected for a caudal view. Total length of the female from Malaysia was 7.7. Cephalothorax 2.76 long, 1.88 wide, 0.66 high. Sternum 1.21 long, 0.9 wide. Abdomen 5.0 long, 1.56 wide. First femur 2.5 long. Chelicerae with 4 pro-

lateral and 3 retrolateral teeth, and approximately 28 denticles in between.

Note.—The immature female holotype of *Perilla cylindrogaster* is darker than the syntypes of *P. teres* from Myanmar, which led Simon to diagnose the new species (Simon 1909: 111): sternum lacks the median light band, and front legs are more or less black. However, the holotype of *Perilla cylindrogaster* is not as dark as the Malaysian specimens, which are clearly conspecific with the syntypes of *Perilla teres*. Coloration intensity thus does not provide appropriate diagnostic characters. On the other hand, somatic morphology and coloration patterns of the immature from Vietnam are identical to those of the syntype of *P. teres*. Lack of differences in general somatic morphology between both species justifies proposing *Perilla cylindrogaster* as a junior synonym of *Perilla teres*.

Additional material examined.—MALAYSIA: Gombak Research Station, Genting Highlands, secondary forest, 5 July 1992, ♀, subadult ♂, C.L. Deeleman, in CD.

Distribution.—Myanmar, Malaysia, Vietnam.

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DO INCREMENTAL INCREASES OF THE HERBICIDE GLYPHOSATE HAVE INDIRECT CONSEQUENCES FOR SPIDER COMMUNITIES?

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ABSTRACT. We examined the indirect effect of the herbicide glyphosate on field margin spider communities. Glyphosate was applied to two replicated ($n = 8$ per treatment) randomized field experiments over two years in 1997–1998. Spiders were sampled using a modified garden vac monthly from May–October in the following treatments: 1997 comprised 90g, 180g, & 360g active ingredient (a.i.) glyphosate ha^{-1} treatments and an unsprayed control; 1998 comprised 360g, 720g and 1440g a.i. glyphosate ha^{-1} treatments and an unsprayed control. We examined the indirect effect of glyphosate on the spider community using DECORANA (DCA), an indirect form of gradient analysis. We subjected DCA-derived Euclidean distances (one a measure of beta diversity and the other a measure of variability), to the scrutiny of a repeated measures ANOVA design. We found that species turnover and cluster variation did not differ significantly between treatments. We attribute the lack of any effect to a large number of common agricultural species which are never eliminated from a habitat, but are instead significantly reduced. Reduction rather than elimination does not cause the spider communities within these plots to turn over any faster than the control. However, like most other animal communities, the spider community did turn over and change in structure and composition through the season, regardless of treatment. Using Spearman rank correlations, we found that this within-season species turnover is related to the decline in vegetation height and the increase in percentage dead vegetation cover in the field margin.

Keywords: Glyphosate, herbicide, spiders, species turnover, DECORANA, field margins

Field margins play an important agricultural role in providing a refuge for beneficial invertebrate predators (e.g., Araneae, some Carabidae; Staphylinidae; Heteroptera) facilitating movements of invertebrates into the crop (e.g., Duelli et al. 1990). Data from herbicide-treated and untreated cereal headlands suggest that butterflies, carabid beetles, Auchenorrhyncha and Heteroptera (Hemiptera) are detrimentally affected by spray applications, but to differing degrees (e.g., Chiverton & Sotherton

1991; Feber et al. 1996; Haughton et al. 1999a,b). This detrimental effect on non-target invertebrates following an experimental spray application of herbicide simulates what may happen when spray is allowed to drift onto non-target areas. Drift may be a product of operator error or a sudden increase in wind speed and in either of these situations, the spray is likely to become misplaced and affect field margins and adjacent semi-natural habitats.

Recent evidence suggests that spider numbers are likely to be significantly affected even by a relatively low rate of herbicide application (Baines et al. 1998; Haughton et al. 1999c). This effect, even at low rates, may

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have detrimental implications for both field margin biodiversity and bio-control programs which use beneficial spiders to control pests. In the context of a rapid increase in worldwide demand for glyphosate when, for example, 70 million hectares of land worldwide were sprayed in 1997 (Woodburn 2000), it is easy to demonstrate a need for a clearer understanding of the potential effect on spiders and other non-target invertebrates.

The properties of glyphosate (*N*-(phosphonomethyl)glycine), an exceedingly effective but slow-acting broad spectrum herbicide, are well known. The herbicide acts by inhibiting the biochemical pathway in plants (i.e., 5-enolpyruvylshikimate 3-phosphate synthase) by blocking the production of aromatic amino acids thus restricting protein synthesis and photosynthetic activity (Bayliss 2000). It is used in a range of agricultural (particularly cereals), industrial and domestic situations to control grasses and other weeds (Woodburn 2000). However, the toxicological effect on invertebrates is little understood except to state that the herbicide is classified as 'harmless' to spiders and a range of other common non-target invertebrates by The Society of Environmental Toxicology and Chemistry (Europe) (Barrett et al. 1994)

In this paper we investigated the within-season effect of incremental levels of glyphosate application (six levels from 90–1440 g active ingredient (a.i) glyphosate ha⁻¹ with a control) on field margin spiders from a community perspective.

METHODS

Study sites.—The field research was based at the Allerton Research and Educational Trust Estate, Loddington, Leicestershire, UK (grid reference: SK 789015). We spread the effort of conducting such a large experiment over two years between 1997–1998. Two field margin study sites were used which were separated by a minor road but were no more than 20 m apart. Both sites had an adjacent dense uncut Hawthorn (*Crataegus monogyna* Jacq.) and Blackthorn (*Prunus spinosa* L.) hedge running along their length. The experimental plot size was the same in both years: field margins were divided into 32 contiguous plots, each measuring 12 m long × 2 m wide.

The 1997 margin was dominated by False Oat-grass (*Arrhenatherum elatius* (L.)) and

Couch-grass (*Elymus repens* (L.)). Eight replicates of four treatments, 90 g, 180 g and 360 g a.i. glyphosate ha⁻¹ (Roundup Biactive, Monsanto, High Wycombe, Berkshire) and an unsprayed control, were randomly assigned along the field margin. Glyphosate was applied to these plots at a volume rate of 200 litres ha⁻¹ and a pressure of 2.5 bar using an Oxford Precision Sprayer fitted with flat fan nozzles on 30.v.1997, during dry and calm conditions (24 °C, RH 55%, wind speed <1 m s⁻¹).

The 1998 margin was dominated by False Oat-grass (*A. elatius* (L.)) and Yorkshire Fog (*Holcus lanatus* (L.)). Eight replicates of four treatments were assigned in a randomized block design: 360 g, 720 g and 1440 g a.i. glyphosate ha⁻¹ (Roundup Biactive, Monsanto, High Wycombe, Berkshire) suspended in water and an unsprayed control. Glyphosate was applied to the plots on the 4.vi.1998 during dry, calm conditions (17.5 °C, RH 84.5%, wind speed <2 m s⁻¹) with the same equipment, volume rate and pressure as that described in 1997.

Data collection.—Spiders were sampled using a modified garden-vac (g-vac) (Ryobi RSV3100E: engine capacity 31 cm³ with a nozzle size 13 cm). The spider samples from each experimental plot comprised 10 sub-samples of 30 second sucks at 1 m intervals along each experimental plot. Sampling was done on the central 10 m of each plot to avoid edge effects from neighboring treatments: the total sampling area per plot approximated to 0.13 m². Each sample of spiders was emptied from the g-vac into a plastic bag, extracted with an aspirator into 70% alcohol and then identified to species level.

Two measures of vegetation structure were taken. Percentage ground cover of dead vegetation in the experimental plots was recorded using permanent 0.25 m² quadrats and, average vegetation height at five positions (as in a domino-5) within the quadrats was recorded to the nearest cm. Three quadrats were positioned at 3 m, 6 m and 9 m within each of the 32 plots and mean percentage dead vegetation cover and mean vegetation height. Spider and vegetation sampling was done monthly between May–October inclusive, to monitor any changes over the season.

Data analyses.—There are many ways of calculating species turnover, but most index-

type methods which have traditionally been used do not take account of the community dynamics as they fail to retain all the information from the species matrix. However, multivariate statistics have been suggested as an inclusive technique which does not oversimplify the dynamic nature of the community (Williamson 1987). We introduce a simple method of calculating species turnover while retaining most of the ecological information from the data matrix. Using DECORANA (DEtrended CORrespondence ANALysis or DCA for short), a widely available package designed specifically for ecological studies to avoid distortions caused by either the arch or horseshoe effects (Hill 1994), *P* values are attached to the turnover rates in DCA-Euclidean space using ANOVAs. This is an extension of Hill's (1994) approximation of the standard deviation of species turnover along the x-axis. Species turnover, which is sometimes referred to as beta (β) diversity, is used here as meaning "the change in the composition of a biological community as a result of either or both the immigration and local extinction of species" (Russell et al. 1995).

First, two binary matrices were created (1997: 58×192 ; 1998: 59×192) which represented the presence/absence of species within each year. These were analyzed separately using DCA (default settings with 26 segments used to remove the arch effect), which arranges points along the axes on the basis of species composition data. Thus, the further two points are from one another in the DCA ordination space, the more dissimilar the spider communities. Once the DCA had produced two biplots (1997 & 1998), the axes 1 and 2 scores were separated into herbicide treatment (i.e., control, 90 g, 180 g etc.). Using the DCA axis 1 and 2 scores, the Euclidean distance for each replicate within each treatment was calculated for consecutive between-month shifts to establish the rate of species turnover. For example, in 1997 for the first replicate in the 90 g a.i. glyphosate ha^{-1} treatment, the following Euclidean distances were calculated from axis 1 and 2 scores: May→June; June→July; July→August; August→September; September→October. Thus, there were five measurements for each of the eight replicates in each of the four treatments ($n = 160$) for both years. These distances indicate the seasonal species turnover in n dimensional space. Ul-

timately, these Euclidean distances indicate the level of species stability (i.e., high or low rates of turnover) between treatments.

We then calculated the average Euclidean distance between all points within the same treatment for each of the months from May–October inclusive ($n = 672$) using the DCA axis 1 and 2 scores for each year (i.e., we generated a distance matrix for each treatment for each month). This approach would indicate whether the size of the cluster varied between treatment. The size of the cluster equates to a measure of community variation; large clusters have more variation in the species complex than small ones.

Univariate repeated measures, with date as the within-subject factor and treatment as the main effect, were used to analyze differences in species turnover (i.e., distance moved in DCA-Euclidean space) and cluster distance throughout the season in each year. As a prerequisite to using a repeated measures ANOVA, we logged ($x + 1$) the data and tested it for sphericity using Mauchly's *W* test. Where significant differences were found between treatments, a Tukey *post hoc* test was used to establish the location of the difference. We also used Monte Carlo randomization tests to establish whether the null hypothesis, that a pattern is present as purely a chance effect of observations in a random order, should be rejected (Manley 1991). Monte Carlo randomizations are useful for verifying the significance level in an ANOVA design when some of the statistical assumptions (i.e., independence) may be in question. The level of significance in a Monte Carlo test is expressed as the percentage of values which are equal to, or higher than can be found in a randomized distribution. If the percentage of values that exceed the observed mean square is less than 5%, then this suggests that the null hypothesis should be rejected. We used 30,000 Monte Carlo randomizations to test this null hypothesis on significant ANOVA test results to check for their validity.

In order to interpret the importance to the arthropod community of the changes in the vegetation caused by the rate of glyphosate, Spearman's rank correlation was used to test for the strength of association between the axis scores and vegetation height and percentage dead vegetation cover.

Table 1.—Araneae species recorded from the field margins at Loddington.

Oonopidae	Araneidae
<i>Oonops domesticus</i> de Dalmas 1916	<i>Lariniodes cornutus</i> (Clerck 1757)
Gnaphosidae	<i>Araniella opistographa</i> (Kulczynski 19505)
<i>Micaria pulicaria</i> (Sundevall 1832)	Linyphiidae
Clubionidae	<i>Ceratinella brevipes</i> (Westring 1851)
<i>Clubiona reclusa</i> Cambridge 1863	<i>Ceratinella scabrosa</i> (Cambridge 1871)
<i>Clubiona lutescens</i> Westring 1851	<i>Walckenaeria acuminata</i> Blackwall 1833
<i>Clubiona compta</i> Koch 1839	<i>Walckenaeria nudipalpis</i> (Westring 1851)
Zoridae	<i>Walckenaeria unicornis</i> Cambridge 1861
<i>Zora spinimana</i> (Sundevall 1833)	<i>Walckenaeria cuspidata</i> (Blackwall 1833)
Thomisidae	<i>Dicymbium nigrum</i> (Blackwall 1834)
<i>Xysticus cristatus</i> (Clerck 1757)	<i>Entelecara erythropus</i> (Westring 1851)
<i>Ozyptila praticola</i> (Koch 1837)	<i>Dismodicus bifrons</i> (Blackwall 1841)
Philodromidae	<i>Gonatium rubens</i> (Blackwall 1833)
<i>Philodromus dispar</i> Walckenaer 1826	<i>Maso sundevalli</i> (Westring 1851)
<i>Philodromus cespitum</i> Walckenaer 1802	<i>Pocadicnemis juncea</i> Locket & Millidge 1953
<i>Philodromus collinus</i> Koch 1835	<i>Oedothorax fuscus</i> (Blackwall 1834)
<i>Tibellus oblongus</i> Walckenaer 1802	<i>Oedothorax retusus</i> (Westring 1851)
Salticidae	<i>Cnephlocotes obscurus</i> (Blackwall 1834)
<i>Euophrys frontalis</i> (Walckenaer 1802)	<i>Monocephalus fuscipes</i> (Blackwall 1836)
Lycosidae	<i>Gongylidiellum vivum</i> (Cambridge 1875)
<i>Pardosa palustris</i> (L. 1758)	<i>Micrargus herbigradus</i> (Blackwall 1854)
<i>Pardosa pullata</i> (Clerck 1757)	<i>Micrargus subaequalis</i> (Westring 1851)
<i>Pardosa prativaga</i> (Koch 1870)	<i>Erigonella hiemalis</i> (Blackwall 1841)
<i>Pardosa amentata</i> (Clerck 1757)	<i>Savignya frontata</i> (Blackwall 1833)
<i>Pardosa nigriceps</i> (Thorell 1856)	<i>Diplocephalus latifrons</i> (Cambridge 1863)
<i>Alopecosa pulverulenta</i> (Clerck 1757)	<i>Diplocephalus connatus</i> Bertkau 1889
<i>Trochosa ruricola</i> (Degeer 1778)	<i>Araeoncus humilis</i> (Blackwall 1841)
<i>Trochosa terricola</i> Thorell 1856	<i>Panamomops sulcifrons</i> (Wider 1834)
Pisauridae	<i>Erigone dentipalpis</i> (Wider 1834)
<i>Pisaura mirabilis</i> (Clerck 1757)	<i>Erigone atra</i> (Blackwall 1833)
Mimetidae	<i>Porrhomma microphthalmum</i> (Cambridge 1871)
<i>Ero cambridgei</i> Kulczynski 1911	<i>Meioneta rurestris</i> (Koch 1836)
<i>Ero furcata</i> (Villers 1789)	<i>Meioneta saxatilis</i> (Blackwall 1844)
Theridiidae	<i>Syedra gracilis</i> (Menge 1869)
<i>Episinus angulatus</i> (Blackwall 1836)	<i>Centromerus sylvaticus</i> (Blackwall 1841)
<i>Theridion bimaculatum</i> (L. 1767)	<i>Centromerita bicolor</i> (Blackwall 1833)
<i>Enoplognatha ovata</i> (Clerck 1757)	<i>Bathypantes gracilis</i> (Blackwall 1841)
<i>Robertus lividus</i> (Blackwall 1836)	<i>Bathypantes parvulus</i> (Westring 1851)
<i>Pholcomma gibbum</i> (Westring 1851)	<i>Diplostyla concolor</i> (Wider 1834)
Tetragnathidae	<i>Poeciloneta globosa</i> (Wider 1841)
<i>Tetragnatha extensa</i> (L. 1758)	<i>Stemonyphantes lineatus</i> (L. 1758)
<i>Tetragnatha montana</i> Simon 1874	<i>Lepthyphantes tenuis</i> (Blackwall 1852)
<i>Pachygnatha clercki</i> Sundevall 1823	<i>Lepthyphantes mengei</i> Kulczynski 1887
<i>Pachygnatha degeeri</i> Sundevall 1830	<i>Lepthyphantes ericaeus</i> (Blackwall 1853)
<i>Meta segmentata</i> (Clerck 1757)	<i>Lepthyphantes pallidus</i> (Cambridge 1871)
<i>Meta mengei</i> (Blackwall 1869)	<i>Lepthyphantes insignis</i> Cambridge 1913
	<i>Neriere clathrata</i> (Sundevall 1830)
	<i>Microlinyphia pusilla</i> (Sundevall 1830)

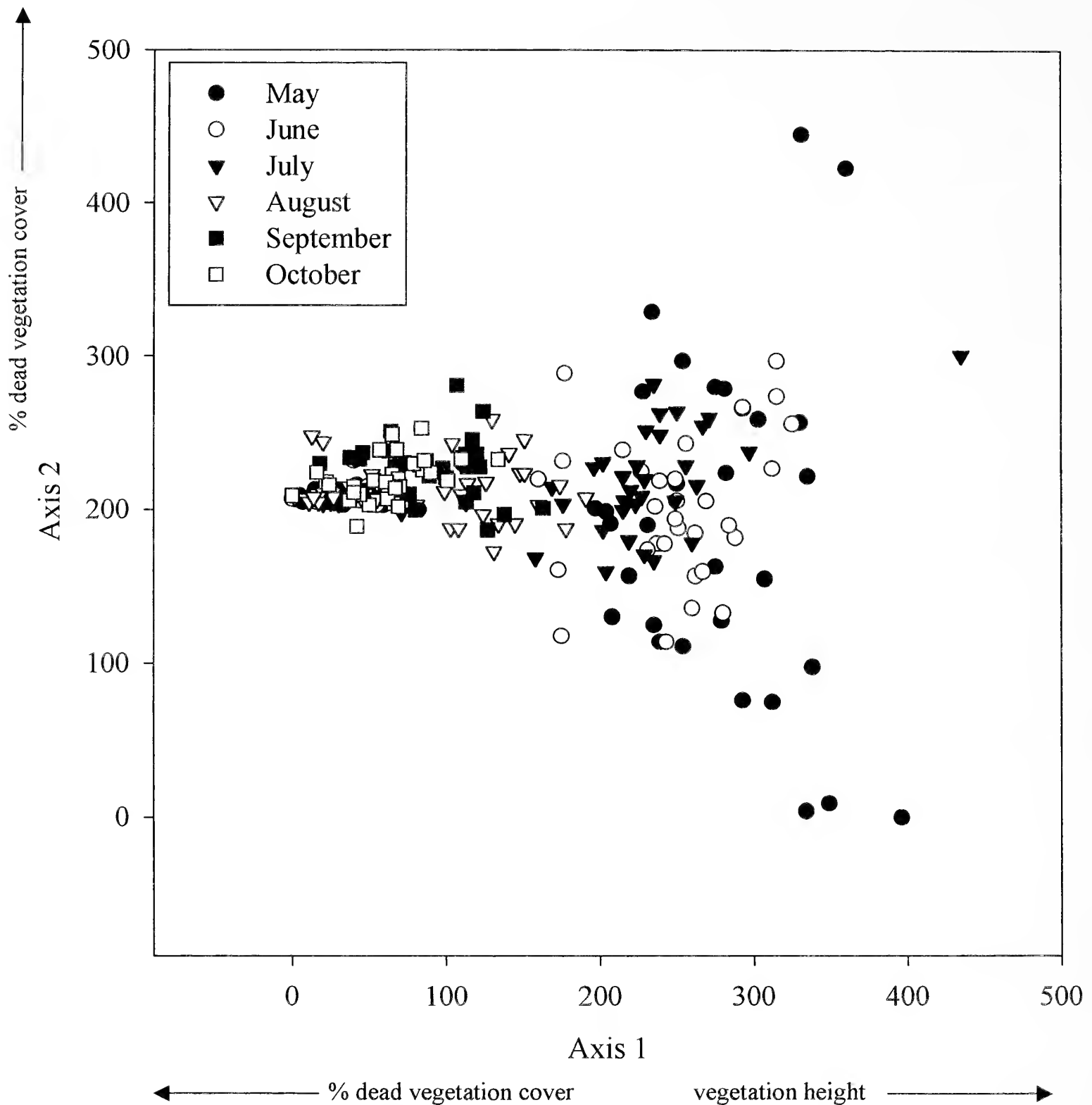


Figure 1.—DCA biplot of 1997 field margin spider samples. (Note: plots indicating symbols as treatments rather than months are not shown because no clear separation can be made between different herbicide rates).

RESULTS

The spider community.—In both 1997 and 1998, the adult spider community was dominated by linyphiids (Table 1). The three species that occurred most frequently (percentage of all the samples in 1997 and 1998 respectively) were *Lepthyphantes ericaeus* (Blackwall 1853) (77.1%; 73.9%), *Lepthyphantes tenuis* (Blackwall 1852) (69.3%; 84.3%) and *Bathyphantes gracilis* (Blackwall 1841) (49.5%; 43.2%), all of which are considered common field margin spiders in Brit-

ain. Between 58 and 59 species were recorded in total in 1997 and 1998 respectively, 44 of which were recorded in less than 10% of the total number of samples for both years, 28 of which were singletons. The total number of spiders recorded in the study was 46,393. Voucher specimens were deposited with Leicester Museum through John Crocker, the county recorder for Leicestershire.

DCA biplots.—No separation along axis 1 or 2 is apparent on either of the 1997 or 1998 biplots (Figs. 1, 2). Instead, all samples form

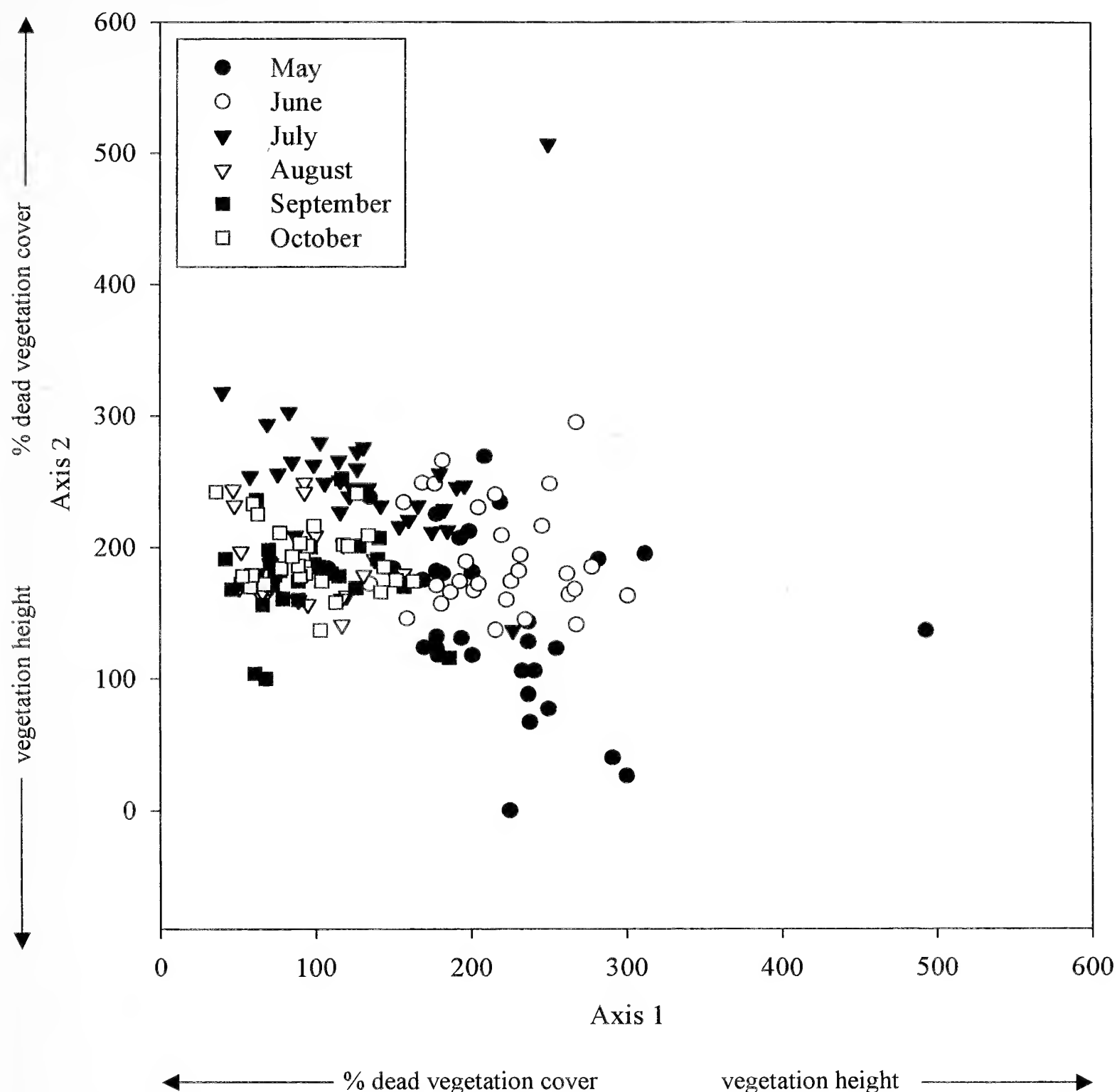


Figure 2.—DCA biplot of 1998 field margin spider samples. (Note: plots indicating symbols as treatments rather than months are not shown because no clear separation can be made between different herbicide rates).

a homogenous cluster, with a tendency for samples within the same month to be aligned. In the 1997 biplot (Fig. 1), axis 1 scores decline as samples move in ordination space through the season. This effect is less discernable in the 1998 biplot (Fig. 2), although samples within each month do aggregate to some extent. The relationship between axis 1 scores and vegetation height and percentage dead vegetation cover indicates significant correlations (Table 2); axis 1 is positively correlated with vegetation height, but negatively correlated with percentage dead vegetation cover in both years. These relationships are reversed

on axis 2 where, apart from a lack of a significant result in 1997 with vegetation height, axis 2 is negatively correlated with vegetation height, but positively correlated with percentage dead vegetation cover in both years.

DCA-Euclidean species turnover.—Species turnover analysis revealed a significant treatment effect in 1997 ($F_{3,28}$ 3.63 $P = 0.024$) but no such effect in 1998 ($F_{3,28}$ 0.24 $P = 0.867$). Significant test results were compared with 30,000 Monte Carlo randomizations and their respective observed mean squares. For the 1997 ANOVA result (i.e., $F_{3,28}$ 3.63 $P = 0.024$), only 0.060% of the randomizations ex-

Table 2.—Spearman rank correlations between vegetation characteristics and DCA axis scores for field margin spiders.

Year	Axis	Vegetation height		Percentage dead vegetation cover	
		r_s	P	r_s	P
1997	1	0.434	<0.001	−0.452	<0.001
	2	−0.753	0.299	0.185	0.010
1998	1	0.477	<0.001	−0.314	<0.001
	2	−0.183	0.011	0.218	0.002

ceeded the observed mean square—strong evidence that observed test results could not be generated randomly.

The differences between treatments in 1997 were due to significantly higher rates of turnover in the 90 g a.i. glyphosate treatments when compared all others (Table 3). Overall, the general trend was for species turnover to decline slightly over the season in 1997 (Fig. 3). The trend in 1998 was much more variable with treatments apparently acting independently of one another (Fig. 4).

DCA-Euclidean cluster size.—Cluster size did not differ significantly over the season between treatment for 1997 ($F_{3,108}$ 1.17 P = 0.327) or 1998 ($F_{3,108}$ 1.45 P = 0.233). The general trend was that cluster size did get smaller over the season in 1997 (Fig. 5) but in 1998, it was more variable with size declining towards the middle of the summer and increasing approaching the end (Fig. 6).

DISCUSSION

DCA biplots and related tests.—Considering all the repeated measures ANOVAs, no consistent monotonic relationship between glyphosate application rate and species turnover or cluster size could be found. The only significant result that was detected in the 90 g a.i. glyphosate ha^{−1} treatment, but this does not compare with the effects measured at higher treatments and thus must be considered a rogue effect. Spider communities did change in many ways over the season (Figs. 1–6), but

this was not related to an incremental increase in the rate of glyphosate application. One major factor which influenced the spider community composition over the season was the profound effect of differences in spider phenology. There is often a marked difference between the composition of the spider community in the spring compared to autumn. July and August are the transition months when spring species disappear (e.g., *Pardosa* species) and autumn species emerge (e.g., *Goniatium rubens* (Blackwall 1833)). However, most of the abundant spiders occurred throughout the whole sampling period; either low in number in spring and more abundant in autumn (e.g., *Bathyphantes gracilis* (Blackwall 1841)) or the reverse (e.g., *Pocadicnemis juncea* Locket & Millidge 1953).

Overall, the response of the spider community was, on first inspection, very different from that of various single species responses observed in other Loddington research. At relatively low rates of glyphosate application (360 g a.i. ha^{−1}), a significant decline in numbers of *L. tenuis* was detected (Haughton et al. 2001a; Haughton et al. 1999c). Similarly, another linyphiid, *G. rubens* was reduced by even lower rates of glyphosate application (180 g a.i. ha^{−1}) and evidence from the same experiment suggests that total spider abundance, and the number of web-spinners are also detrimentally affected (Haughton et al. 1999c).

Table 3.—Tukey P values for differences between mean DCA-Euclidean distances for field margin spiders in the 90 g a.i. glyphosate ha^{−1} treatment when compared with all other individual treatments.

	Control	90 g a.i. glyphosate ha ^{−1}	180 g a.i. glyphosate ha ^{−1}	360 g a.i. glyphosate ha ^{−1}
Mean	73.32	141.10	92.80	93.62
P	0.002	—	0.037	0.040

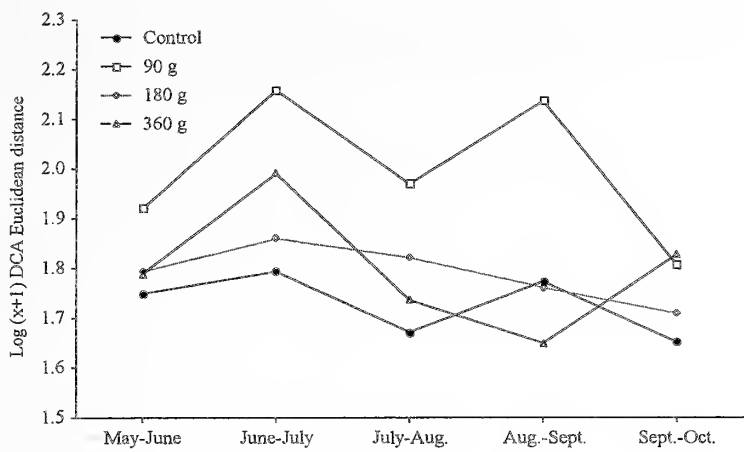


Figure 3.—The mean ($n = 160$) seasonal spider species turnover between glyphosate treatments in 1997 showing moderate variability within the season and the lack of a single trend. (Note: this graph should not be used to located differences between treatments, please refer to statistics in Table 2).

The question arises then, why are the measures of species turnover and cluster size not showing a similar trend? The answer lies with the way in which spiders respond, even to the highest rate of glyphosate application. As detailed earlier from previous experiments at Loddington, although spiders were shown to be significantly reduced, they were never completely eliminated (see Haughton et al. 1999c; Haughton et al. 2001a). This constant species presence was apparent in the lack of any significant differences in either the species turnover or cluster size results, suggesting that there was little variation in the composition of the spider community, whatever the herbicide treatment. This lack of variation may indicate that an active aerial spider community is “blanketing out” any treatment ef-

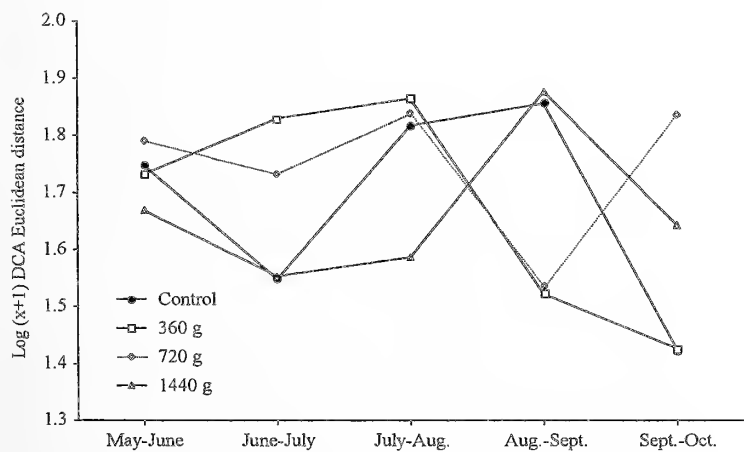


Figure 4.—The mean ($n = 160$) seasonal spider species turnover between glyphosate treatments in 1998 showing the large variability within the season and the lack of a single trend. (Note: this graph should not be used to located differences between treatments, please refer to statistics in the text).

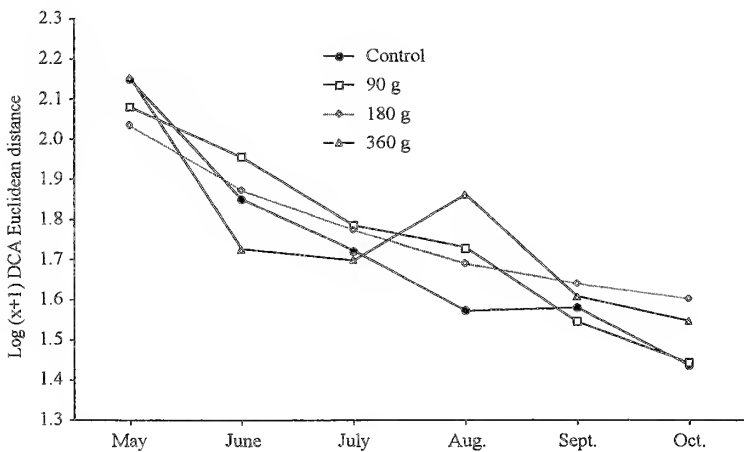


Figure 5.—The mean ($n = 672$) seasonal decline in spider community DCA-Euclidean cluster size between glyphosate treatments in 1997 showing the trend of variable decline in cluster size through the season. (Note: this graph should not be used to located differences between treatments, please refer to statistics in the text).

fects. The great majority of spiders from the Loddington species list (78%) have a propensity to balloon, either in their immature phase (e.g., *Pardosa* species) or throughout their lives (i.e., most Linyphiidae and some Theridiidae and Tetragnathidae) (e.g., Duffey, 1956; Meijer, 1977). The ability to balloon will undoubtedly have affected the rate at which the different spider communities turn over, causing the differences between treatments to be blurred by a constant aerial fallout or emmigration.

Exposure to herbicides reduces weed cover and diversity (e.g., de Snoo & van der Poll 1999), which in turn reduces the habitat qual-

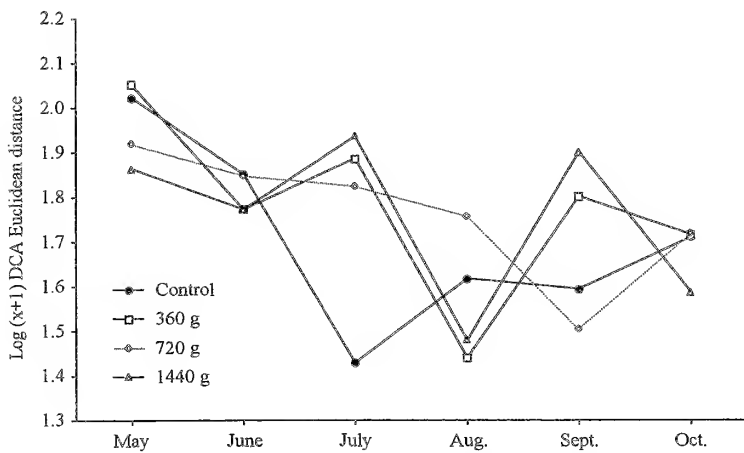


Figure 6.—The mean ($n = 672$) seasonal decline in spider community DCA-Euclidean cluster size between glyphosate treatments in 1998 showing the trend of variable decline in cluster size through the season until August–October when clusters become larger. (Note: this graph should not be used to located differences between treatments, please refer to statistics in the text).

ity for the spiders, and consequently their numbers decline. Recently, using the spider *L. tenuis*, we demonstrated that at relatively low rates of glyphosate application in the field ($360 \text{ g a.i. ha}^{-1}$), a significant decline in numbers of *L. tenuis* was detected (Haughton et al. 2001a). The herbicide was not shown to act as an insecticide in direct toxicity tests, even at very high rates of glyphosate application ($2160 \text{ g a.i. ha}^{-1}$), but indirectly through habitat degradation: poisson regression showed that numbers of *L. tenuis* were related (non-linear) to vegetation height and percentage dead vegetation cover (Haughton et al. 2001a,b). The same two variables, vegetation height and percentage dead vegetation cover, were also found to be significantly related to the spider community along axes 1 and 2 in this experiment (Table 2). It is undeniable that vegetation structure has a profound effect on spiders (Uetz 1991). Various studies have demonstrated a relationship between spiders and vegetation height (e.g., Döbel et al., 1990; Rushton & Eyre 1992) and selection of dead vegetation by spiders has also been noted (e.g., Duffey 1962; Gibson et al. 1992). However, vegetation height and percentage dead vegetation cover were only correlated with the change in the spider community over the season, not with the difference between treatments as there were no cluster divisions by treatment in either of the DCA ordinations.

Implications of incremental increases of glyphosate.—Based on our previous research, incremental increases of glyphosate have caused a significant reduction in numbers at the species level, between guilds and for total numbers. From this perspective, the spider community is detrimentally affected by applications of this herbicide. However, in terms of effect on the composition of the spider community, the answer is less clear; species were not eliminated from herbicide treated margins and thus there would seem less cause for concern. However, perpetual use of glyphosate at high rates during the growing season may contribute to a sustained reduction in species, particularly for those species which are not *r*-statists.

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GENITALIC POLYMORPHISM—A CHALLENGE FOR TAXONOMY

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ABSTRACT. Genitalic polymorphism (including polymorphism of secondary sexual characters) is a typical example of a phenomenon that found no place in taxonomy as there was no framework to place it. Neither the speciation models used in ecology nor the species concept currently in use with taxonomists “allowed” species to have discontinuously polymorphic genitalia. Recent developments in ecological modeling that make sympatric speciation acceptable, and changing ideas about sexual selection, both imply genitalic polymorphism in particular circumstances. According to the mate check hypothesis the presence of hidden but crucial new adaptive characters is checked during courtship and mating. Sympatric speciation with changing behavioral characters without shifts in somatic traits, goes through a phase of intraspecific polymorphism during which the mating module obtains new traits backing up the newly acquired hidden character. It implies that this speciation process ends with the alteration of the recognition module. After the completion of the speciation process, cases of atavism with loss of behavioral adaptations through deleterious mutations or reversions and reappearance of ancestral genital characters, are expected to occur regularly. Without these, the mate check mechanism would be meaningless. A number of examples of both types of genitalic polymorphism in arachnids are presented. It explains why genitalic polymorphism is rarely observed although it might be a common phenomenon.

Keywords: Atavism, female choice, mate check, sexual selection, species concept, relapse, teratology

So far, aberrant specimens have been considered a rare phenomenon and the result of unusual “mistakes” of nature. The statement of Sorkin (1982) is symptomatic of the general attitude towards these occurrences: “. . . anomalies and teratologies do occur naturally and the taxonomist should be aware that species have been described from these freaks of nature . . .”. Specimens with deviating morphology have indeed often been called teratologies almost by definition. Yet, there is a clear difference between polymorphism and teratology. The latter phenomenon is morphologically characterized by asymmetry and uniqueness. If large numbers of teratologies are studied (Mitov 1995; Curcic et al. 1995) similar or identical cases may be found but these must be considered as the inevitable result of chance. Polymorphism on the other hand has a genetic origin and has been defined by Ford (1953) as follows: “The occurrence together, in the same habitat, of two or more discontinuous forms of a species, the rarest of which is too frequent to be maintained merely by recurrent mutation.” So teratology and polymorphism are vastly different phenomena.

As intraspecific polymorphism, and genitalic polymorphism in particular, cannot be dismissed as natural errors, their occurrence has long been problematic. The reason for that is the general application by taxonomists of the phylogenetic species concept. This concept defines species as “the smallest diagnosable sample of self perpetuating organisms” (Wheeler & Platnick 2000) which these authors argue to be the only workable concept to date. This species concept, together with the dismissal of sympatric speciation (Coyne 1992; Rice & Hostert 1993), prevented a sound interpretation of the rare cases in which genitalic polymorphism was observed, sometimes as a spin-off from research involving a breeding program. Yet, in some exceptional cases, certain researchers have accepted that a polymorphic phase in speciation exists (Tabachnik et al. 1979; Emberton 1995) but so far no such explanations have been reported in arachnology. Now that the concept of sympatric speciation gains adherents and has become much more acceptable thanks to recent models (Kondrashov & Kondrashov 1999; Dieckmann & Doebeli 1999, referred to as the KK and DD models by Tregenza & Butlin

1999) even taxonomists subscribing to the phylogenetic species concept reckon with the occurrence of polymorphism (Wheeler & Platnick 2000).

Predictions of the mate-check hypothesis, formulated for the first time by Jocqué (1998) and detailed in Jocqué & Szûts (2001), do expect genitalic polymorphism to occur during the process of speciation as well as after the completion of the process through a phenomenon here referred to as “relapse”, which is a particular type of atavism. The present paper is a purely theoretical essay that aims at cornering the framework in which both genitalic polymorphism with more or less stable incidence and the occurrence of rare specimens with aberrant genitalic characters, so far considered as “teratologies,” can be placed.

MATING AND RECOGNITION MODULES

It is accepted (Eberhard 1996) that the timing of the female decision about what male or what sperm will be selected for egg fertilization, varies to a large extent from one species to the other. In many species the choice occurs before proper mating and is then called “overt choice” whereas in many others the selection is made after copulation, a phenomenon called “cryptic choice.” As a consequence, the decision may be dependent upon a wide array of possible signals emitted by the male. The most common signals are apparently tactile and are emitted during mating itself. These are emitted by the genitalia or secondary genitalic structures. In many animals though, the crucial information may be transmitted by visual (mating dances), auditory (stridulation) or chemical (pheromones, gustatorial) types of courtship, often by combinations of two or more of these, but before mating takes place. In order to facilitate the discussion about the many aspects that may be involved in the transfer of information during courtship and mating, we introduced the term “mating module” which encompasses all the means by which information is exchanged (Jocqué & Szûts 2001).

In analogy, the term “recognition module” is here introduced. It concerns the mechanisms for exchange of the information that enables individuals to recognize conspecifics. On average the recognition module tends to be much smaller than the mating module and

is emitted to a similar extent by both sexes. It enables possible partners to quickly recognize the identity of a partner before they engage in time and energy consuming proper mating. Pheromones in general and pheromone impregnated silk (Tietjen & Rovner 1982; Jackson & Cooper 1990; Pollard et al. 1987) are excellent examples of such modules in spiders.

THE MATE CHECK HYPOTHESIS

Students of the niche theory differ in their views on speciation from those who study sexual selection. Adaptation to, and shifts in ecological niches are paramount with the former (e.g., Southwood 1978), rapid evolution of sexual characters (SC, including secondary sexual characters), supposedly molded by female choice, are more important for the latter (see Andersson 1994, for a review). One of the reasons for these unrelated or even opposite views is that in some speciose taxa, e.g. *Hortipes* Bosselaers & Ledoux (Bosselaers & Jocqué 2000), *Storena* Walckenaer (Jocqué & Baehr 1992), *Diores* Simon (Jocqué 1990), the only morphological differences between species appear to be in the SC. This might give the impression that speciation has occurred without the development of adaptive novelties other than improved stimulation of the female (Eberhard 1985, 1994, 1996) or as a result of sexual conflict (Parker & Partridge 1998; Arnqvist 1998; Arnqvist et al. 2000). Therefore the cause for speciation is sought in the evolution of these SC alone and female choice is assumed to be the driving force behind speciation. In these hypotheses, abstraction is made of behavioral or other hidden adaptations which may be subject to profound changes but often have no bearing on somatic morphology. The weakness of these hypotheses is that they do not have an explanation for the persistence of the species with less complex genitalia.

The “mate check” hypothesis on the other hand links elements of the theories of the “niche” and “sexual selection” (Jocqué 2000) and assumes that evolution through behavioral adaptation, allowing more efficient use of underexploited resources, is backed up by changes in the mating module. The presence of these crucial characters is checked, hence “mate check,” during courtship and mating. This line of thinking may explain the

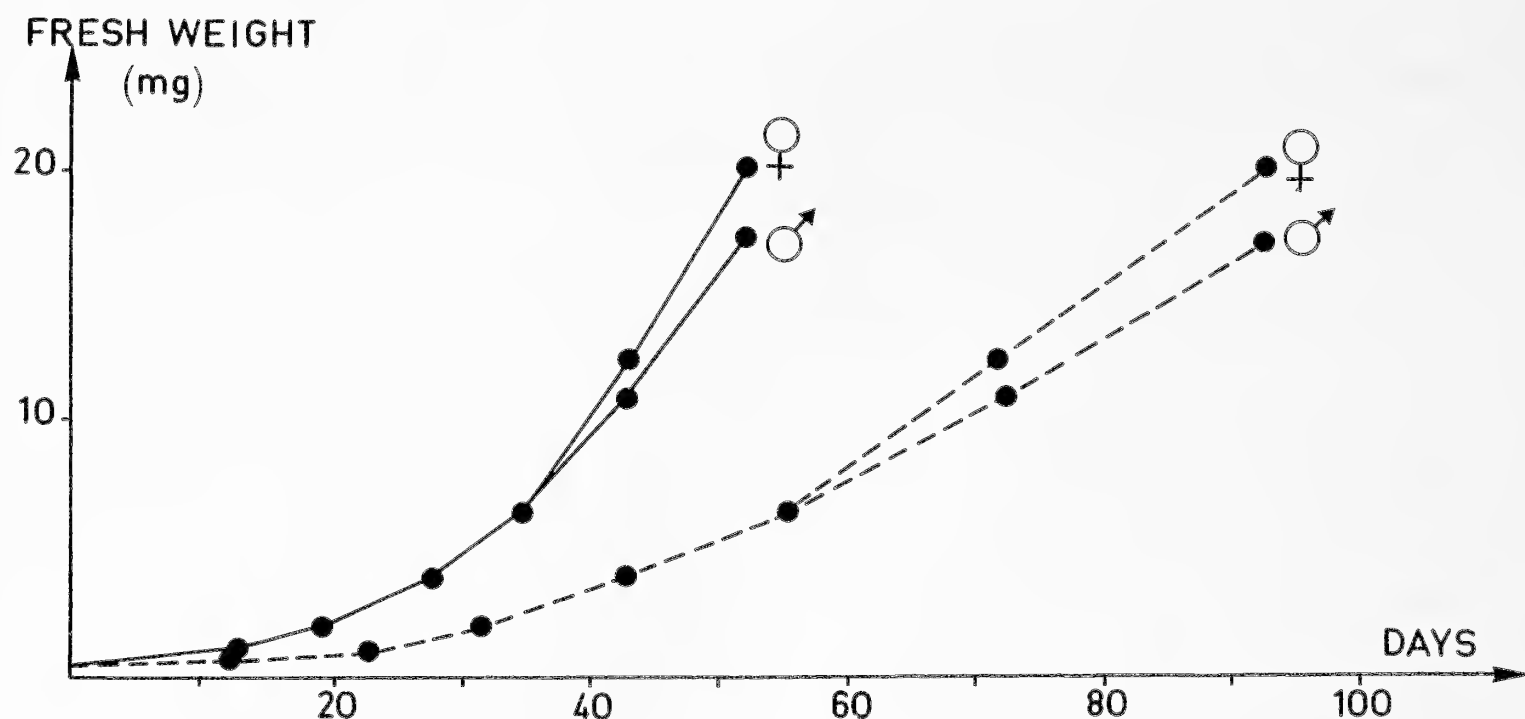


Figure 1.—Development rate of spiderlings of *Pardosa injucunda* hatched from a single egg case; remarkable is the occurrence of two well separated cohorts of which the fastest needs almost only half as much time as the slow cohort to reach adulthood (after Célérier, 1981).

large range of complexity of SC in closely related and somatically often indistinguishable taxa, implying that complexity of SC is linked to ecological specialization. It also predicts that in the case of a speciation event, the original species persists in what is called the source (optimal habitat) whereas the newly evolved species thrives in the sink (marginal habitat) thanks to a new adaptation.

The core of the “mate check” hypothesis is a mechanism that guarantees gamete exchange with a partner that possesses recently acquired behavioral or other hidden characters. The need for such a mechanism is based on the observation that losses of new adaptations through deleterious mutations are remarkably high (Gould & Lewontin 1979; Lande 1994). Hidden adaptations are often nothing else than preference for a particular microhabitat and these differences are obviously difficult to demonstrate, certainly when they are present within a single, albeit polymorphic, population. Different habitat preference has been shown though for conspecific morphs of certain Lepidoptera (Jones et al. 1993), Diptera (Tabachnik et al. 1979) and fishes (McPhail 1964). Hawthorne & Via (2001) showed that there is genetic linkage between ecological specialization and reproductive isolation through host choice in pea aphids. In populations without polymorphism but in which the first step to speciation has occurred, the new adaptation is even more dif-

ficult to show. An excellent example of a hidden character in spiders is found in Célérier (1981) who reports on the breeding results for the west African lycosids *Brevilabus gillorum* Cornic 1980 and *Pardosa injucunda* O.P.-Cambridge 1876 (Fig. 1). In both species, spiderlings from the same egg cocoon were found to grow at very different rates and to form two clearly separated cohorts. *Pardosa injucunda* reached adulthood either after 50 days for the fast cohort or after 100 days for the slow one. The fast development can be considered an adaptation to marginal habitats or periods where the rainy season is shorter than in the optimal condition, in which a development time of 100 days is fast enough. Slow development has the advantage that the life cycle can be completed efficiently even when prey is scarce (Jocqué 1983). But as there is not the slightest morphological difference between the two groups, this adaptation must be considered as “hidden”.

SYMPATRIC SPECIATION UNDER THE MATE CHECK MECHANISM

The mate check hypothesis clearly assumes sympatric speciation, a speciation model that has gained support in recent literature. Especially the “KK” and “DD” models (see above) stress the occurrence of a polymorphic phase of genitalic characters and the fact that speciation needs changes in multiple loci. In our diagram (Fig. 2) these changes are repre-

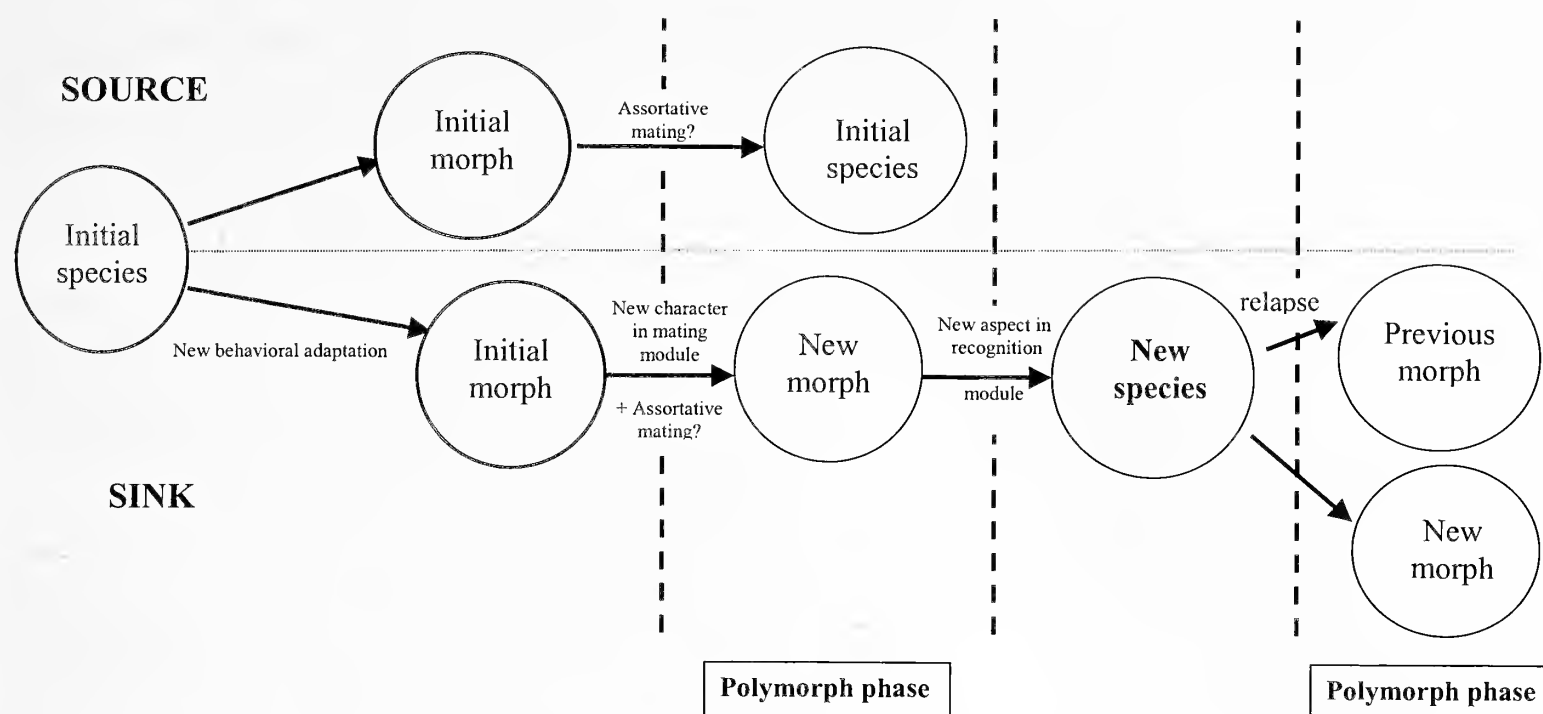


Figure 2.—Diagrammatic model of sympatric speciation according to the mate check hypothesis. Part of a population is able to breed successfully in a former sink thanks to the acquisition of a new, hidden adaptation, later backed up by a new character in the mating module. Assortative mating might not be necessary as there is disruptive selection as a result of the distorted survival rate in the source and sink subhabitats; in the former sink, mate check will further reduce the breeding success of specimens that do not have the new linked characters. Speciation is completed by the modification of the recognition module. The initial or an atavistic morph may reappear due to relapse (deleterious mutations or reversions) eliminating the behavioral adaptation and its linked trait in the mating module. It should be noted that two phases of genitalic polymorphism are expected.

sented by a new adaptive trait, a new trait in the mating module and a modification of the recognition module.

Polymorph phase.—The hypothesis coincides well with the findings of Rice & Chipindale (2001) who state that sex may play an important role in consolidating beneficial mutations as suggested in Jocqué (1998).

The reason for the chronology of the sequence—new behavioral character—new aspect of mating module—modification of recognition module, has to do with the observation that the morphology of the genitalia themselves does very often not prevent copulation and that, in many cases, if not all, recognition takes place before copulation or courtship commences (Jackson 1987; Jackson & Cooper 1990; Pollard et al. 1987) sometimes even before the sexes meet. This observation may even lead to a new species concept which defines a species as “a population whose members share a unique recognition module”.

The mate check mechanism only makes sense if there is a real risk for mating with a partner that has lost a critical hidden adaptation and together with it the linked aspect in

the mating module. This means that we must expect to come across specimens, males as well as females, that have a mating module, which in many cases means sexual organs, differing from what is found in “normal” specimens and which we will call “relapses.” Since the differences must be discontinuous, it should be very easy to recognize these specimens. Yet, the present habit to define species exactly on the base of discrete differences, not linked by intermediates in a morphocline, has prevented the detection of relapses. It is therefore likely that the specimens with relapse that have reached adulthood and have been found, are hidden in the literature as separate species!

EXAMPLES OF POLYMORPHISM

Pre-speciation polymorphism.—Although many cases of assumed incipient speciation in sympatry have been reported, very few examples mention the combined change of behavior and morphology in conspecific morphs. The few studies mentioned above and those of Müller (1957) on *Euscelis* (Homoptera) and Meyer (1989) on *Cichlasoma citrinellum* (Pisces) are among the few exceptions. But if sympatric speciation is as common as as-

sumed by some authors (Tregenza & Butlin 1999) we may be surrounded by a multitude of polymorphic species in the course of speciation, of which the different morphs are considered as heterospecific. A perfect example is the case of *Oedothorax gibbosus* (Blackwall 1841) and *O. retusus* (Westring 1851) (Linyphiidae) that have been described as different species on the basis of discrete differences in the shape of the male carapace (see Table 1). Although they were already suspected to be conspecific by Simon (1926) they were only proven to be so by De Keer & Maelfait (1988). Maelfait *et al.* (1990) and Heinemann & Uhl (2000) further specified the details of this case of polymorphism. Van Acker *et al.* (2002) recently found that the morphs have different ecological optima that are congruent with the predictions of the hypothesis. Another case is that of *Pelecopsis janus* Jocqué 1984 (Linyphiidae), a spider species with dimorphic males from South Africa. These male forms were described in the same species as the samples only contained one type of female and the male palps of both forms are identical (Jocqué 1984). *Troxochrus scabriculus* (Westring 1851) and its form *T. scabriculus cirrifrons* (O. P.-Cambridge 1871) are another example of dimorphic males (Müller 1984). Recently Huber & Gonzalez (2001) described the new species *Siboneya anthraia* Huber & Gonzalez 2001 (Pholcidae) in which the conspecific female morphs, obtained in a breeding program, have different epigynes. Other possible candidates for dimorphic females are *Drassodella vasivulva* Tucker 1923 and *Drassodella septemmaculata* Strand 1909, described as separate species by Tucker (1923) from the Cape in South Africa. The male of the second species is still unknown. Yet large pitfall samples only contain one male form and high numbers of both female forms. Since males of ground spiders are without exception always more abundant than females in pitfall samples, it is assumed that the somatically identical females of these *Drassodella* species are conspecific (Jocqué, pers. obs.).

These few examples prompt the following reflections: the detection of polymorphism is either based on male secondary sexual characters (male carapace shape) or female characters. In all these cases, the identity of the male, based on its palpal characters that are supposed to be the final criterion for species

diagnosis, has given rise to the initial suspicion that one was dealing with polymorphic species. But if different males were found with very similar or identical females, these would be cataloged as different species without hesitation. The following questions arise: Do males with polymorphic copulatory organs occur and if so, how frequent are they? Are there species in which both females and males are polymorph? And does this kind of polymorphism indeed represent a stage in sympatric speciation?

Post-speciation polymorphism, atavism or relapse.—Appearance of rare aberrant forms are usually dismissed as teratologies. Yet, rare aberrant specimens, when symmetrical, do not fit the definition of teratology nor that of polymorphism (Ford 1953). For that reason we here adopt the term “relapse,” defining a type of atavism that implies loss of an aspect of the mating module together with a hidden adaptation.

Very few cases of apparent relapses are known most probably because the conditions to find them were not available. One of the most spectacular cases is that of *Bryantella smaragdus* (Crane 1945) (Scioscia 1995 and figures therein). This author raised spiderlings from egg batches produced by females collected in the wild. Among the offspring from one cocoon she found no less than four types of somatically identical males with palps with discontinuous differences mainly in the length of the embolus and the shape of the tibial apophysis. Three types of females with discontinuous differences in the epigyne were obtained. Each of the morphs was represented by several specimens. The phenomenon was observed in the offspring obtained from several cocoons. According to the presently prevailing custom in spider taxonomy, the extremes, with, as the most spectacular difference, the length of the embolus, would be placed in different genera. One of the less spectacularly aberrant morphs, collected in the wild had indeed been described in a different genus. Chickering (1946) described the new species *Parnaenus convexus* which now appears to be one of the morphs of *Bryantella smaragdus* (Scioscia 1988). Yet, in the same paper Chickering describes another species of *Bryantella* but did thus not realize these species were very closely related. It is important to note that the morph described by Chicker-

Table 1.—Overview of cases of genitalic polymorphism and specimens with aberrant genitalic characters in spiders.

Taxon	Num ber of mor phs	Sex and number involved	Characters involved	Situation	Source
Pre-speciation polymorphism					
<i>Oedothorax gibbosus</i> (Blackwall 1841)	2	M	cephalothorax shape	synonymy with <i>O. tuberosus</i> shown by breeding	De Keer & Mael- fait 1898; Maelfait et al. 1990; Heine- mann & Uhl 2000
<i>Pelecopsis janus</i> Jocqué 1984	2	M	cephalothorax shape	suspected intra- specific poly- morphism	Jocqué 1984
<i>Troxochrus scabriculus</i> O.P.-Cambridge 1851	2	M	cephalothorax shape	suspected intra- specific poly- morphism with <i>T. s. cirrifrons</i> (O.-P. Cam- bridge 1871)	Müller 1984
<i>Drassodella septemmaculata</i> (Strand 1909)	2	F	epigyne	suspected conspe- cific with <i>D. vasivulva</i> Tuck- er 1923	unpublished
<i>Siboneya anthraia</i> Huber & Gonzalez 2001	2	F	epigyne	polymorphism shown by breeding	Huber & Gonza- lez 2001
Relapses					
<i>Pardosa amentata</i> (Clerck 1757)	2	5 M	male palp	described as f. <i>ileachensis</i> of <i>P. amentata</i>	Beaumont 1991
<i>Pardosa palustris</i> (L. 1758)	3	2 F	epigyne	recognized as ab- errant conspecif- ic	Bergthaler 1997
<i>Pardosa agrestis</i> (Westring 1861)	3	F	epigyne	recognized as ab- errant conspecif- ic	Samu (pers. comm.)
<i>Bryantella smaragdus</i> (Crane 1945)	4	17 M	male palp	1 morph de- scribed as <i>Par- naenus convex- us</i>	Scioscia 1988, 1995
<i>Bryantell asmaragdus</i> (Crane 1945)	3	22 F	epigyne	1 morph described as <i>Parnaenus convexus</i>	Scioscia 1988, 1995
<i>Bacelarella tentativa</i> Szûts & Jocqué 2001	2	2 M	male palp	described as sepa- rate species, suspected re- lapse of <i>B. con- jugans</i>	Szûts & Jocqué 2001
<i>Bacelarella pavida</i> Szûts & Jocqué 2001	2	4 M	male palp	described as sepa- rate species, sus- pected relapse of <i>B. conjugans</i>	Szûts & Jocqué 2001

ing was found in Panama, whereas the females used by Scioscia came from southern Brazil. The differences between the morphs are strictly discontinuous and no intermediates linking the different morphs were found. No differences in behaviour between the different morphs were observed.

Aberrant symmetrical spiders, most often males, have been encountered in the wild and either treated as different species as in the case of *Bryantella*, as separate "form" (*Pardosa amentata* f. *ileachensis*, Beaumont 1991) or as enigmatic morphs in *Pardosa palustris* (L. 1758) (Bergthaler 1997) and *Pardosa agrestis* (Westring 1861) (F. Samu, pers. comm.). In each of these cases, several specimens were found, either in the same population or far apart. The differences from the typical morph were always discrete.

According to the mate check hypothesis, similar cases should be common, at least in somatically stable taxa with a wide range of variation in the genitalia. For two reasons the chance to detect such morphs is fairly small. First of all these morphs are likely to be rare. As the loss of a genitalic trait is supposed to imply the loss of a crucial behavioral (hidden) character, it is to be expected that only in unusually favorable circumstances, will the specimen with relapse reach adulthood. Second, we do not expect species to be polymorphic at least not in such a way as to present clearly discontinuous differences. Scanning the literature of revisions and faunas, one comes across quite a number of "rare species" that have been described on one or a few specimens, often of one sex and found among numerous specimens of a related species. In the present context it is not an exaggeration to suggest that the identity of such species should be controlled.

The case of *Bacelarella* Berland & Millot 1941 illustrates this. In rain forest in Ivory Coast, seven syntopic species of litter dwelling salticids belonging to the genus *Bacelarella* (Szûts & Jocqué 2001) were found. They are somatically very similar and apparently adapted to life in the poorly lit forest floor environment. They represent an amazing morphocline with increasingly complex genitalia (Jocqué & Szûts 2001), the most simple ones are very rare and respectively two and four specimens have been collected in a two year pitfall sampling campaign combined with

sticky traps, sweeping and hand collecting. The position of both of these species on a cladogram (unpublished) as derived from a species with more complex genitalia, strengthens the suspicion that these might be relapses of the "ancestral" species.

The chance to come across these specimens is less remote in a laboratory breeding program. The artificial circumstances encountered in the laboratory may be considered as ecological relaxation. Even specimens with reduced fitness as a result of the loss of adaptive characters may be able to reach adulthood in such a situation. That these cases have even been overlooked in laboratory breeding programs, is not surprising either. Since one expects animals from the same parents to have the same diagnostic characters, these characters are usually not verified. It is taken for granted that they are all the same. As a control will most often need detailed observation of genitalia, it is not evident that differences, albeit discrete, are detected, unless the program is especially set up for that purpose.

Although genitalic polymorphism is only rarely observed, the cases that are presented here might be examples of two phenomena that are not rare at all: prespeciation polymorphism and relapse.

The only way we can find the answers to these questions is to look back to the past and try to find out how many species have been described on conspecific polymorphic morphs. It is evident that this will not be a simple process and that in many cases either a breeding program or molecular analysis will be needed to obtain the answer.

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THE FIRST GALLIENIELLIDAE (ARANEAE) FROM EASTERN AFRICA

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ABSTRACT. *Toxoniella*, a new genus of Gallieniellidae is described from forest remnants on the Taita Hills in Kenya. The genus is characterized by legs with well developed spination, the male palp with posterior tegular extension not containing the spermduct and the epigyne with a single central frontal ledge, double spermathecae, and cul de sac tubes in front. Two new species, both known from males and females, are recognized: *T. taitensis* and *T. rogoae*. The position of the genus is discussed in the light of the presence of enlarged piriform gland spigots on the ALS in the male and its close relationship to *Drassodella* supported by a number of synapomorphies.

Keywords: Eastern Arc, Kenya, lamelliform hairs, piriform gland spigots

The Gallieniellidae is a small spider family created by Millot (1947) for a single species (*Gallieniella mygaloides* Millot 1947) of remarkable Araneomorphae with spectacularly porrect chelicerae from Madagascar. The family was for the first time defined by Legendre (1967). For quite some time the family was considered to be endemic to the large island even after the revision of Platnick (1984) who added a second genus (*Legendrena* Platnick 1984) and some species from islands in the neighborhood of Madagascar, but belonging to the same zoogeographical area. However, Platnick (1990) expanded the family, mainly on the base of the morphology of the spinnerets and included *Drassodella* Hewitt 1916 from the Cape region in South Africa. At the same occasion more taxa were announced from Australia, which drastically changed the initial endemic status of the family. Recently Goloboff (2000) described another new gallieniellid genus, *Galianoella* Goloboff 2000, from Argentina.

During recent field work in forest remnants of the Taita Hills in Kenya, at the far northern edge of the Eastern Arc Mountains, a number of gnaphosoid spiders were collected in which the females obviously lack the typical enlarged piriform gland spigots (EPGS) of the

Gnaphosidae. The ALS have a sclerotized subdistal ring instead and are slightly conical and closely set. However, males appear to have EPGS. The chelicerae of these spiders are slightly porrect, more clearly so in the males and the habitus is very similar to that of *Drassodella*. This combination of characters would indicate that we are dealing with representatives of the Gallieniellidae, a find greatly expanding the range of the family on the African continent.

METHODS

The following abbreviations are utilised: * (after a number) = spines in a row, ALE = anterior lateral eyes, ALS = anterior lateral spinnerets, AME = anterior median eyes, AW = anterior width (of the MOQ), d = dorsal, disp = dispersed, dw = distal whorl, EPGS = enlarged piriform gland spigots, EM: embolic membrane; F = femur, L = length of the median ocular quadrangle, MA = median apophysis, MOQ = median ocular quadrangle, Mt = metatarsus, P = patella, pl = prolateral, PLE = posterior lateral eyes, PME = posterior median eyes, PW = posterior width (of the MOQ), PS = posterior spinnerets, rl = retrolateral, T = tibia, TE = tegular extension, v = ventral.

The following acronyms are used: AMNH = American Museum of Natural History, New York; MRAC = Musée Royal de l'Afrique

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Centrale, Tervuren; NMK = National Museums Kenya, Nairobi.

All measurements are in mm.

TAXONOMY

Toxoniella new genus

Type species.—*Toxoniella taitensis* new species.

Diagnosis.—Specimens of *Toxoniella* have far more spines than representatives of Madagascan Gallieniellidae. Male representatives of *Toxoniella* have an oval tegulum with a posterior extension but lack a tegular central ridge; the embolus as well as the median apophysis and the embolar membrane are short and simple; females are characterized by the epigyne with long cul de sac tubes in front of the spermathecae which are double, each pair consisting of two well separated spheres.

Etymology.—The name is derived from the Greek *τοξον* which means arch, and refers to the presence of the taxon in the Eastern Arc mountains. The gender is feminine.

Natural history.—All specimens were caught in mountain forest by pitfall traps, sieving litter or hand collecting. Some of these forests are tiny remnants not exceeding a few ha. The elevation distribution ranges from 400–1200 m.

Affinities.—The position of *Toxoniella* is problematic in that the females fit the Gallieniellidae (absence of EPGS) whereas the males should be placed in the Gnaphosidae as they possess these typical spigots. However, the Gallieniellidae have thus far only been defined (Platnick 1990) by the absence of EPGS piriform gland spigots and the presence of a distal sclerotized ring on the ALS, both plesiomorphic characters. In the absence of a sound definition of the Gallieniellidae there are two possibilities for the placement of *Toxoniella* both of which imply that they are in fact intermediate between the Gallieniellidae and the Gnaphosidae. The genus can either be regarded as a derived gallieniellid in which only the males have acquired EPGS or as an ancestral gnaphosid in which the females have not yet acquired EPGS and retained a distal sclerotized ring in females. A third possibility exists that would consider *Toxoniella* a derived gnaphosid in which the EPGS have reversed into a distal sclerotized ring in females. The latter possibility is difficult to maintain for two rea-

sons. The reversal of the EPGS into a previously lost sclerite is a most unlikely evolutionary step and the genus is apparently related to the South African *Drassodella* in which both sexes lack EPGS. This relationship is the main argument to accommodate *Toxoniella* among the gallieniellids. These genera share the dense spination that is absent in the Madagascan members of the family, rows of lamelliform hairs under the tarsal claws (Figs. 18–21), a pair of prolateral abdominal sigilla (see figs. 32, 33 in Jocqué 1999) and frontal cul de sac expansions in the epigyne (Figs. 8, 12). In *Drassodella* these are bladder-like whereas they are clearly longer than wide in *Toxoniella*. Both the genera further possess a posterior extension of the tegulum, not connected with the origin of the embolus as in *Gallieniella*. The main differences in the pair of African continental genera is the absence of a central tegular ridge in *Toxoniella*, present in *Drassodella* and pairs of well separated spermathecae present in the former, absent in the latter, where the spermathecae appear to be constricted.

Description.—Small to medium-sized spiders (3–9) with oval carapace, widest between coxae II and III; narrowed in front to about 0.65 times maximum width. In profile rather flat, thoracic area lower than cephalic one, highest point just behind posterior eyes. Cervical grooves poorly indicated. Color: prosoma, including chelicerae and legs yellowish brown, covered with short, brownish golden setae; abdomen gray with dense cover of brownish golden setae. Eyes in two recurved rows, subcircular and subequal, except PME smaller oval and flat. Clypeus low, slightly more than diameter of ALE, straight with few setae. Chilum single, triangular. Chelicerae only slightly prolonged, extending forward about one fifth of carapace length (the variable individual inclination makes this figure not very relevant). Endites fairly broad, smoothly constricted opposite insertion of trochanters. Sternum shield-shaped with dispersed setae; coxae IV narrowly separated. Labium slightly longer than broad; hardly widened at base. Legs: formula 4123. Spination: fewer spines on anterior leg pairs than on posterior pairs. TI and TII, sometimes PI and PII, in male with ventral rows of long recurved setae. Mt III and IV with poorly developed preening brush. Claws with about 3–7 teeth, more nu-

merous on anterior legs. With two rows of up to 6 lamelliform setae under claws (Figs. 20, 21). No scopulae. Abdomen oval, without scutum in both sexes; frontal part of male abdomen slightly sclerotized. Four dorsal sigilla and one small lateral one on either side. Six spinnerets: ALS in females with sclerotized subdistal ring, slightly conical, closely set; piriform gland spigots well developed but not enlarged (Figs. 15, 16); males with some EPGS (Fig. 17), without sclerotized distal ring. Male palp: tibia with small dorsolateral apophysis. Tegulum with posterior extension, not containing the sperm duct and frontal tapered extension. Embolus, median apophysis and embolar membrane all short and simple. Epigyne with single, wide, frontal ledge and curved lateral grooves; entrance ducts short but with frontal cul de sac tubes in front of double spermathecae.

Distribution.—Only known from the Taita Hills, southeastern Kenya.

Toxoniella taitensis new species

Figs. 1–8, 15–17, 20, 21

Type material.—Holotype male, Kenya, Taita Hills, Mwachora Forest, 3°24'S 38°22'E, March–April 1999, 1600 m, mountain forest, pitfall, L. Rogo (MRAC 208858, now in NMK). Paratypes: 2 females, Taita Hills, Ronge Forest, 3°21'S 38°25'E, 28 October–13 November 1998, 1350 m, mountain forest, pitfall, L. Rogo (MRAC 208794); 1 ♀ 1 juvenile: Taita Hills, Ngangao Forest, 3°22'S 38°20'E, 1720 m, mountain forest, pitfall trap, 24 March 2000, R. Jocqué & C. Warui (MRAC 209662); 1 ♂, 1 ♀, as previous (MRAC 209523); 2 ♂, 2 ♀, Taita Hills, Ngangao Forest, 3°22'S 38°20'E, 1750 m, mountain forest, pitfall trap, 15 July 1998, L. Rogo (MRAC 208887 1 ♂, 1 ♀ in NMK); 4 ♂, 1 ♀, 4 March 1999, further as previous (MRAC 210047, 2 ♂ in AMNH); 1 ♂, 1 juvenile, Tsavo West, Kasigau, 3°49'S 38°40'E, 2–9 December 2000, 1102 m, mountain forest, sieved litter, R. Jocqué (MRAC 209956); 2 ♀, Taita Hills, Vuria Forest, 3°24'S 38°17'E, 28 March 2000, 2100 m, mountain forest, sieved litter, R. Jocqué (MRAC 209552); 1 ♀, Taita Hills, Chawia Forest, 3°22'S 38°20'E, pitfall trap, 13–18 May 1998, L. Rogo (MRAC 208804); 1 ♀, Taita Hills, Yale Forest, 3°39'S 38°33'E, 6 December 1999, 1800 m, mountain forest,

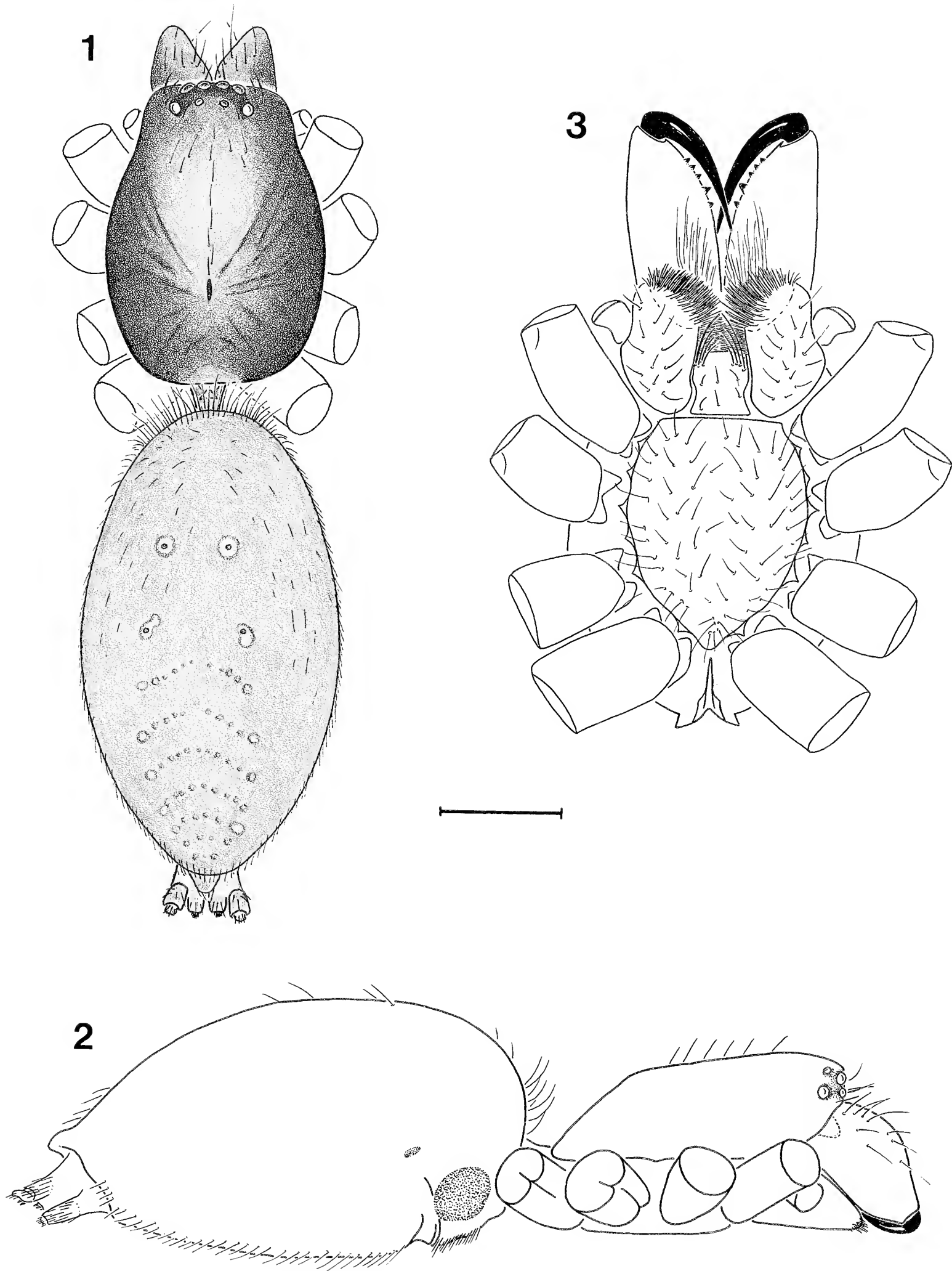
winkler extraction of litter, VandenSpiegel & Michiels (NMK).

Etymology.—The species' name refers to the type locality.

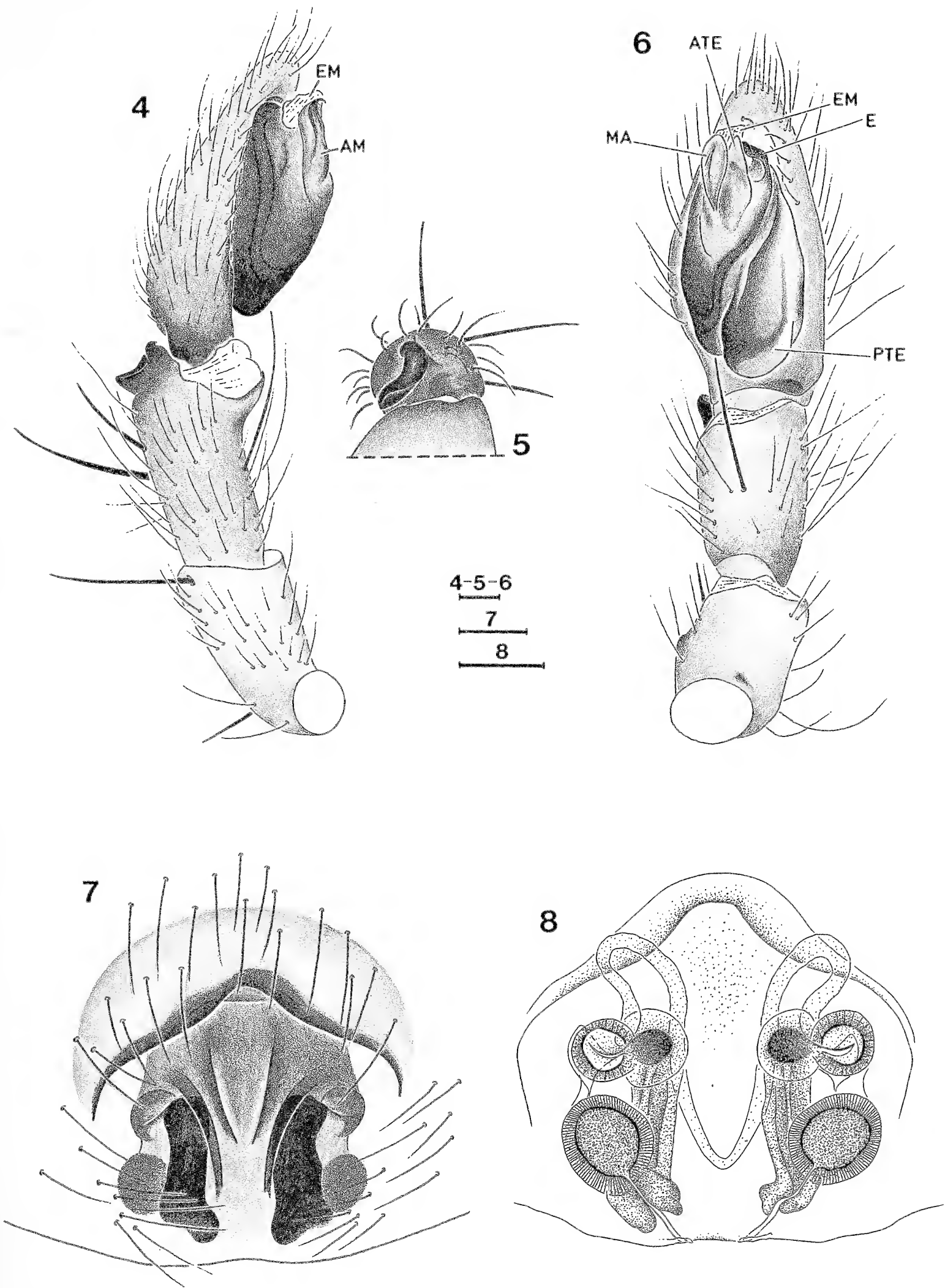
Diagnosis.—The male of this species is recognized by the presence of a frontal, tapered tegular extension between the embolus and the MA and the ridge-shaped frontal apophysis on the tibia. The females are characterized by the epigyne which is as wide as long, has a pronounced anterior ledge with sinuous rim and long cul de sac extension of the copulatory ducts which reach the anterior margin of the epigyne.

Male (**holotype MRAC 208858; range of other males in parentheses**).—Total length 6.39 (4.54–7.38). *Carapace*: 2.70 (2.13–2.98) long, 1.92 (1.49–2.13) wide. Carapace yellowish brown, with very faint darker pattern, paler in front of fovea. *Abdomen*: gray, slightly reddish in front, with dense cover of brownish golden setae. *Eyes*: AME: 0.10; ALE: 0.11; PME: 0.10; PLE: 0.11; AME–AME: 0.05; AME–ALE: 0.02; PME–PME: 0.10; PME–PLE: 0.11; MOQ: AW: 0.22; PW: 0.29; L: 0.26. Clypeus low, slightly less than diameter of ALE. Chilum triangular, 0.11 high, 0.19 wide. *Legs*: Spination: I: F pl1d3* P–T v1–1–2 Mt v2–2–1; II: F pl1d3* P–T v1–1–2 Mt v2–2; III: F pl1d2*rl1 P–T pl2*d2*rl2*v2–2–2 Mt 10disp dw6; IV: F pl1d2*rl1 P v1 T pl2*d1rl2*v2–2–2 Mt 10disp dw6. T, P and F of anterior leg pairs with ventral rows of long curved setae. *Palp* (Figs. 4–6): palpal tibia with dorsolateral apophysis as curved ridge; tegulum with posterior protrusion, not containing sperm duct, with frontal tapered extension between short, curved embolus and elongate, spoon-shaped median apophysis.

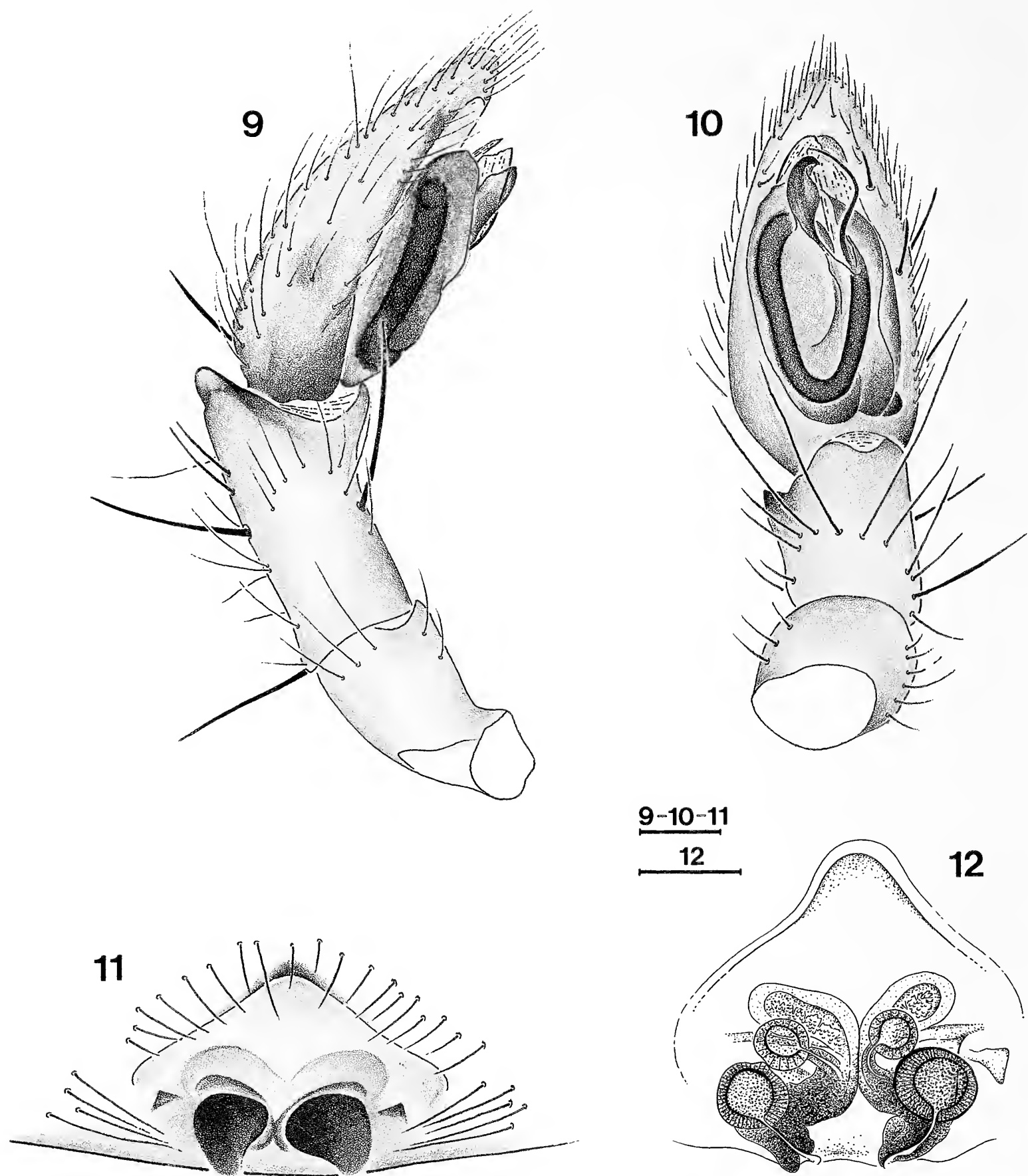
Female (**paratype MRAC 209522, range of other females in parentheses**).—Total length 7.81 (6.60–8.38). *Carapace*: 3.05 (2.49–3.83) long, 2.34 (1.92–2.41) wide. *Carapace* (Figs. 1–3): as in male. Abdomen gray, with dense cover of brownish golden setae. *Eyes*: AME: 0.18; ALE: 0.14; PME: 0.11; PLE: 0.16 AME–AME: 0.05; AME–ALE: 0.04; PME–PME: 0.14; PME–PLE: 0.14; MOQ: AW: 0.34; PW: 0.37; L: 0.34. *Clypeus*: low, half the diameter of ALE. *Chilum*: triangular, much wider than in male and less well delimited. 0.10 high, 0.51 wide. *Legs*: Spination: I: F pl1d2* P–T–Mt v2–1; II: F



Figures 1–3.—Female *Toxoniella taitensis* new species. 1, habitus, dorsal; 2, habitus, lateral; 3, prosoma, ventral view. Scale line: 1 mm.



Figures 4–8.—*Toxoniella taitensis* new species. 4, male palp, retrolateral view; 5, frontal view of tibia; 6, male palp, ventral view; 7, epigyne, ventral view; 8, epigyne, cleared, dorsal view. ATE: anterior tegular extension, E: embolus, EM: embolic membrane, MA: median apophysis, PTE: posterior tegular extension. Scale lines: 0.1 mm.



Figures 9–12.—*Toxoniella rogoae* new species. 9, male palp, retrolateral view; 10, male palp, ventral view; 11, epigyne, ventral view; 12, epigyne, cleared, dorsal view. Scale lines: 0.1 mm.

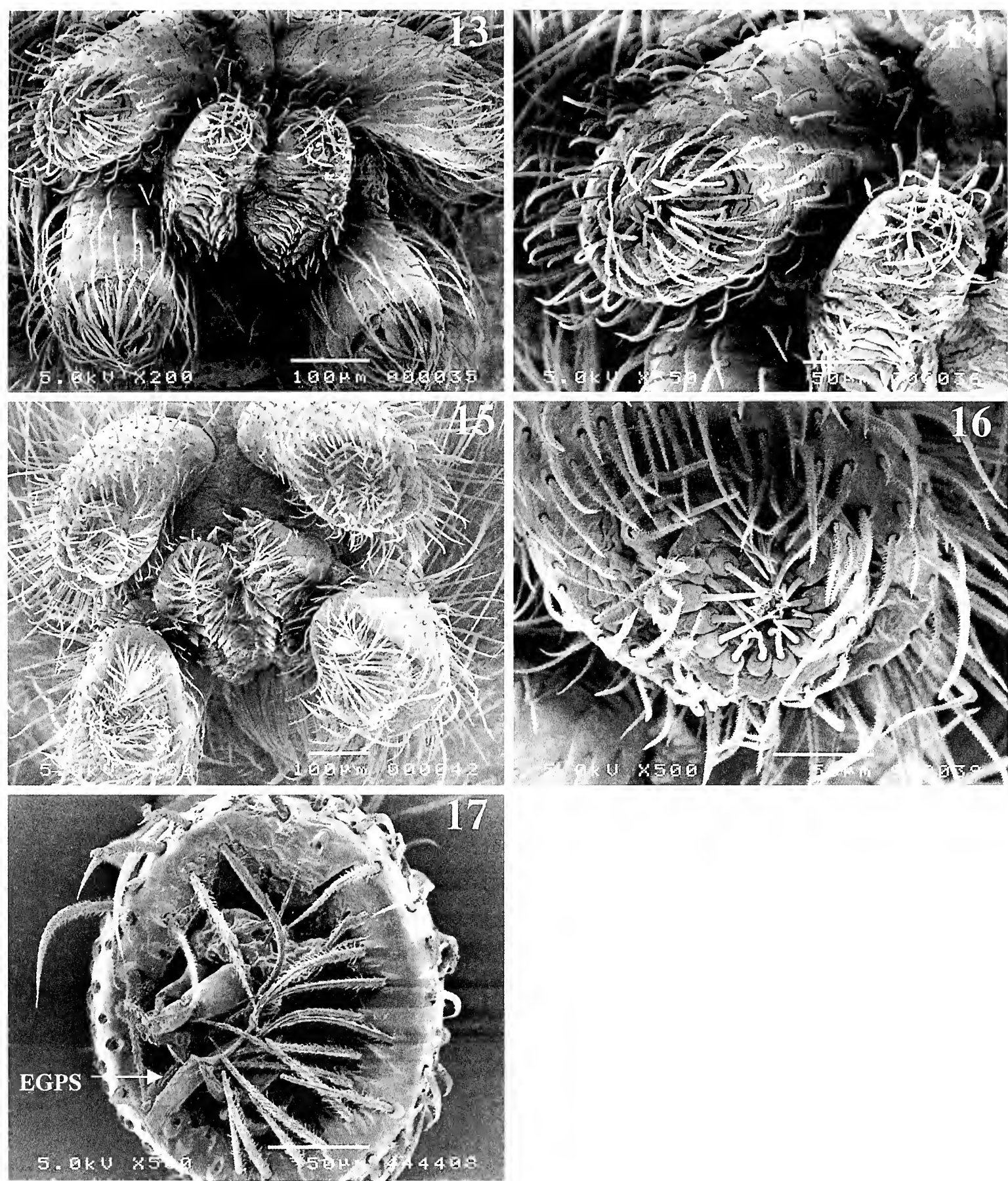
pl1d2* P–T v1 Mt v2–1; III: F pl2*d2*rl2* P–T pl2*d2*rl2*v2–2–2 Mt 10disp dw6; IV: F pl2*d2*rl2* P–T pl2*d2*rl2*v2—2–2 Mt 10disp dw6. *Epigyne* (Figs. 7, 8): with wide sinuous, frontal ledge, central longitudinal groove and widely separated longitudinal entrance openings. Entrance ducts short and parallel, running towards the front, with wide slightly curved cul de sac tubes, reaching an-

terior margin of epigyne; two well separated globular spermathecae.

Distribution.—Taita Hills, Kenya.

Toxoniella rogoae new species
Figs. 9–12

Type material.—Holotype: Male: Kenya, Taita Hills, Ngangao Forest, 3°22'S 38°20'E, 1750 m, mountain forest, pitfall trap, 15 July

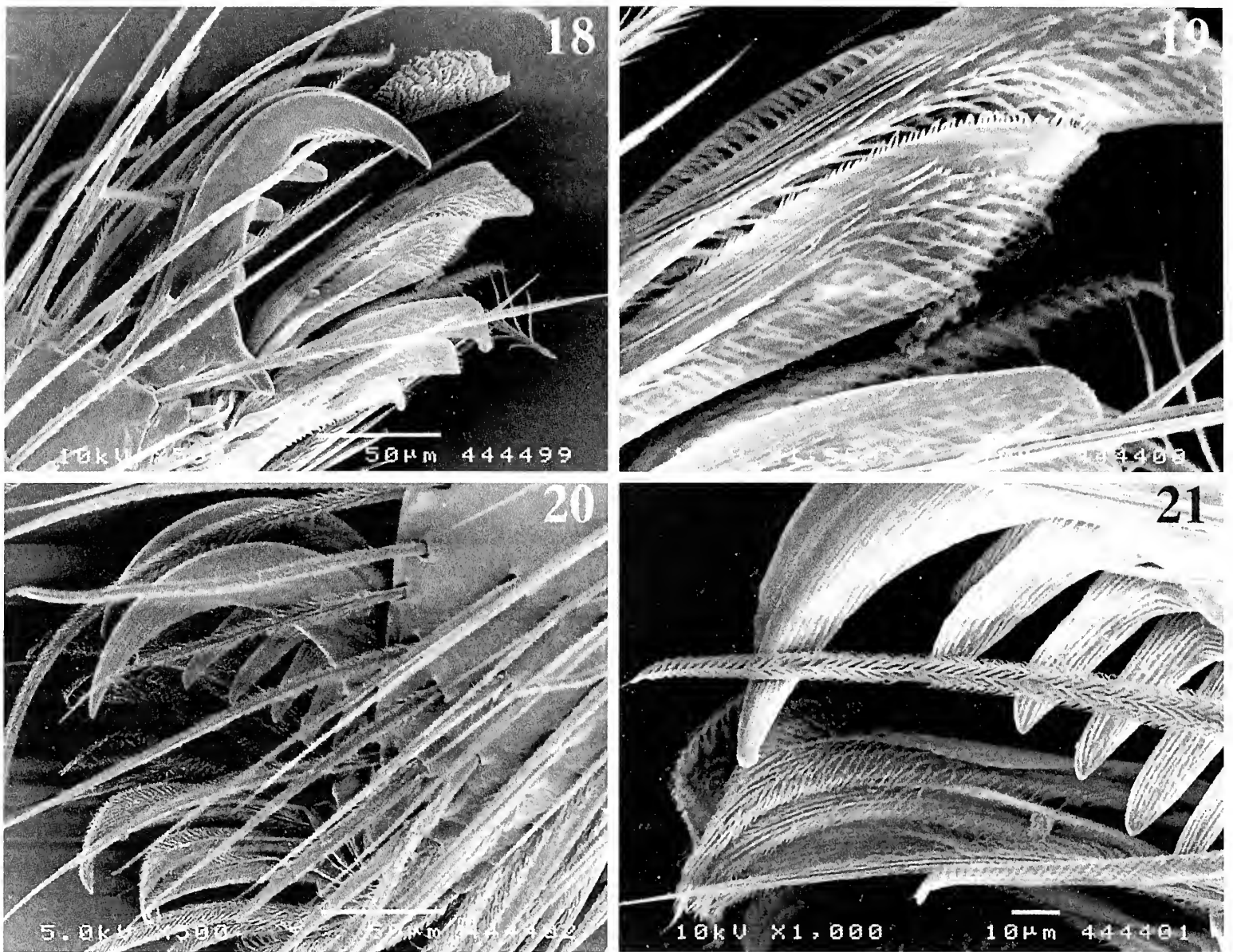


Figures 13–17.—*Drassodella vasivulva* Tucker, female 13, spinnerets; 14, right ALS. *Toxoniella taitensis* new species, female 15, spinnerets; 16, left ALS; 17, male, right ALS showing EGPS (enlarged piriform gland spigots). Scale lines: 100 µm (13, 15) and 50 µm (14, 16, 17).

1998, L. Rogo (MRAC 209914, now in NMK). Paratypes: 1 ♂, 1 ♀: Ngangao Forest, 3°22'S 38°20'E, 1720 m, mountain forest, pitfall trap, 24–26 March 2000, Jocqué & Warui (NMK); 1 ♀: same data as holotype (MRAC 209661); 2 ♂: Ngangao Forest, 24–26 March 2000, 1720 m, pitfalls, Jocqué & Warui (NMK).

Etymology.—The species' name is a patronym in honor of Lucy Rogo (ICIPE) who carried out a pitfall trapping program in the Taita Hills and collected the first Gallieniellidae there.

Diagnosis.—The male of this species is recognized by the short, blunt, dorsolateral tibial apophysis and the embolus with a trans-



Figures 18–21.—*Drassodella vasivulva* Tucker. 18. Lamellate setae under tarsal claws; 19, Idem, detail; *Toxoniella taitensis* new species. 20, Lamellate setae under tarsal claws; 21, Idem, detail. Scale lines: 10 μ m (19, 21) and 50 μ m (18, 20).

lucent appendage; the female is characterized by the short epigyne in which the cul de sac expansions of the copulatory ducts do not reach the anterior margin.

Male (holotype).—Total length 3.20. *Carapace*: 1.63 long, 1.18 wide; brownish yellow. *Abdomen*: gray, slightly brownish in front, with dense cover of brownish golden setae. *Eyes*: AME: 0.06; ALE: 0.10; PME: 0.06; PLE: 0.10; AME–AME: 0.03; AME–ALE: 0.02; PME–PME: 0.06; PME–PLE: 0.07; MOQ: AW: 0.16; PW: 0.19; L: 0.17. *Clypeus*: low, less than half diameter of ALE. *Chilum*: triangular, 0.06 high, 0.16 wide. *Legs*: Spination: I: F d2* P–T–Mt v1; II: F d2* P–T v1 Mt v2–1; III: F pl2d2*r11 P–T pl2*d1rl2*v1–2–2 Mt 9disp dw5; IV: F pl2d2*r11 P–T pl2*d1rl2*v1–2–2 Mt 10disp dw5. TI with two, TII with one, ventral rows of three to five long curved setae. *Palp* (Figs. 9, 10): palpal tibia with dorsolateral apophysis which is a

blunt, short extension. Tegulum with small posterior extension, not containing sperm duct. Embolus short, sinuous, with hyaline retrolateral appendage; median apophysis short, curved.

Female (other female in parentheses).—Total length 3.21 (5.11). *Carapace*: 1.63 (2.20) long, 1.21 (1.59) wide; Carapace and remainder of prosoma brownish yellow. *Abdomen*: oval; gray with dense cover of brownish golden setae. *Eyes*: AME: 0.06; ALE: 0.08; PME: 0.05; PLE: 0.10 AME–AME: 0.02; AME–ALE: 0.02; PME–PME: 0.08; PME–PLE: 0.06; MOQ: AW: 0.14; PW: 0.18; L: 0.14. *Clypeus*: low, 0.6 times the diameter of ALE. *Chilum*: triangular, very poorly delimited. *Legs*: Spination: I: F d2*—P–T v1; II: F d2*—P–T v1; III: F pl2*d2*r11 P–T pl2*d1rl2*v2–2–2 Mt 8disp dw5; IV: F pl2*d2*r11 P–T pl2*d1rl2*v2–2–2 Mt 8disp dw5. *Epigyne* (Figs. 11, 12): with wide,

strongly recurved, frontal ledge, widely separated oval entrance openings. Entrance ducts short, running towards the front, with wide cul de sac tubes, strongly curved outward, not reaching anterior margin of epigyne; two well separated globular spermathecae.

Distribution.—Taita Hills, Kenya.

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THE OCCURRENCE OF ABDOMINAL URTICATING HAIRS DURING DEVELOPMENT IN THERAPHOSINAE (ARANEAE, THERAPHOSIDAE): PHYLOGENETIC IMPLICATIONS

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ABSTRACT. The occurrence of abdominal urticating hair types throughout juvenile development is studied in five Uruguayan theraphosid species of different genera. Adults of three of these species have urticating hairs of Types III and IV while the other two species have Types III and I. Considering spider size as an estimator of development, Type I or IV occurred early, in small juveniles, while Type III hairs always occurred after the other types during development. The homology of urticating hairs and their use in phylogenetic studies of Theraphosinae is discussed. Sexual dimorphism in the occurrence of urticating hair types is analyzed and a hypothetical explanation is proposed.

RESUMEN. La presencia de pelos urticantes abdominales a través del desarrollo es estudiada en juveniles de cinco especies de terafósidas uruguayas de géneros diferentes. Los adultos de 3 de estas especies presentan pelos urticantes tipo III y IV mientras que las otras dos presentan los tipos III y I. Considerando el tamaño como indicador del desarrollo los tipos I o IV aparecen tempranamente mientras que los pelos tipo III ocurren siempre después que los otros tipos, durante el desarrollo. Se discute la homología de los pelos urticantes y su uso en la filogenia de Theraphosinae. Se propone una explicación para el dimorfismo sexual encontrado en estos pelos para algunas especies de terafósidas.

Keywords: Theraphosinae, urticating hairs, theraphosid ontogeny, theraphosid phylogeny

Abdominal urticating hairs of theraphosid spiders were thoroughly described by Cooke et al. (1972), and are only present in New World subfamilies. These authors described four morphological types of urticating hairs: Type II found only in Aviculariinae and Types I, III and IV present in Theraphosinae. Arboreal Aviculariinae transfer the urticating hairs by direct contact (Bertani & Marques 1996) while Theraphosinae release urticating hairs by friction of the hind legs against the abdomen, as a defensive behavior (Cooke et al. 1972; Pérez-Miles & Prandi 1991; Bertani & Marques 1996). Urticating hair types were used by Pérez-Miles (1992, 2000) and Pérez-Miles et al. (1996) for phylogenetic analysis of the Theraphosinae. The co-occurrence of Type III with Type IV or Type III with Type I in the same individual caused the homology of these to be questioned and consequently put into question their use as a multistate character; for this reason they were coded as three independent presence/absence characters by these authors. Bertani & Guadanucci (1999) found hairs of intermediate morphology between Type III and Type IV and between Type

III and Type I in adults. They proposed serial homology and polarized Type III hairs as plesiomorphic. Sexual dimorphism in the occurrence of urticating hair types was reported by Bertani (1997) for some theraphosid species where males have Types I and III while females have only Type I. Pérez-Miles (2000) also reported that *Iracema cabocla* Pérez-Miles 2000 males have Types III and IV while females only have Type IV.

This study tries to determine: 1. the order of occurrence of urticating hairs during development, and 2. if the sexual dimorphism is caused by a loss of a hair type by females or if it is gained by males during development. Five species of Theraphosinae from Uruguay were studied: *Acanthoscurria suina* Pocock 1903, *Eupalaestrus weijenberghi* (Thorell 1894), *Grammostola mollicoma* (Ausserer 1875), *Homoeomma uruguayense* (Mello-Leitão 1946) and *Plesiopelma longisternale* (Schiapelli & Gerschman 1942). Adults of the two former species have Types I and III urticating hairs while adults of last three species have Types III and IV (Pérez-Miles et al.

1996). The phylogeny of urticating hairs is discussed in light of present results.

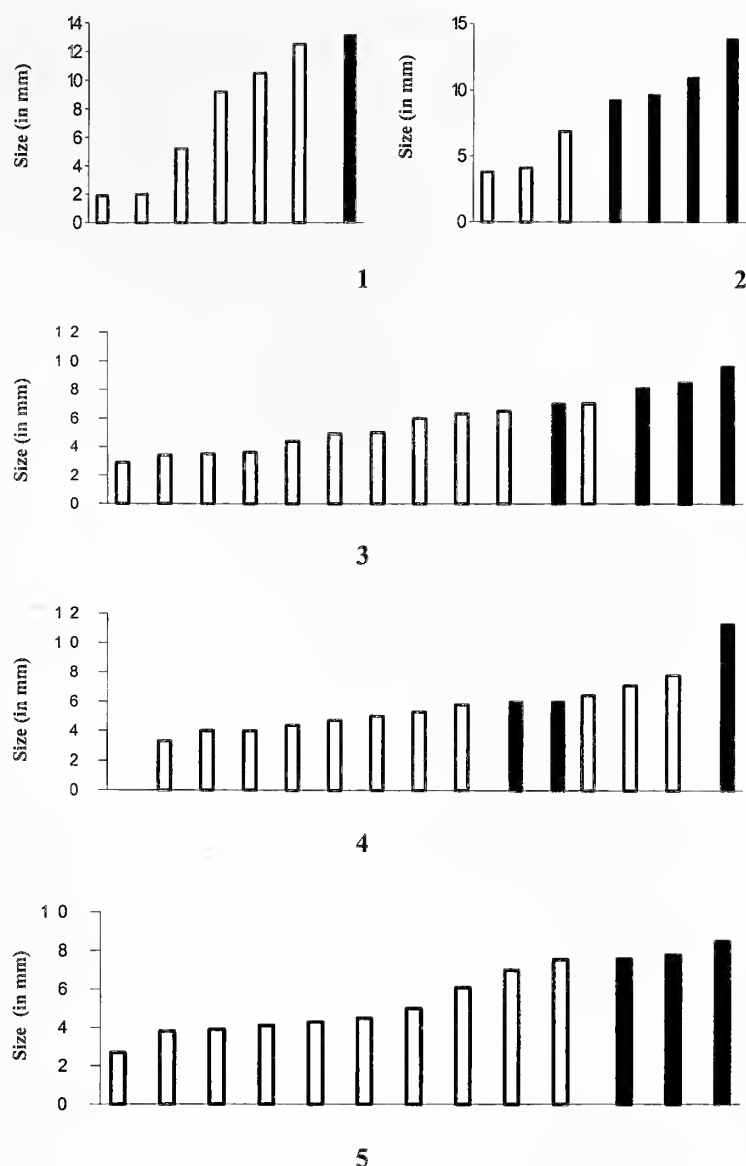
METHODS

Fifty-nine juvenile to adult specimens of different sizes were examined and deposited in the arachnological collection of Facultad de Ciencias, Montevideo, Uruguay. These individuals belong to the following species: *A. suina* (7 individuals), *E. weijenberghi* (8), *G. mollicoma* (15), *H. uruguayense* (16), and *P. longisternale* (13). Live juveniles were identified to species mainly using their chromatic patterns, general morphology, ecological characteristics and collection site. Although juvenile identification is usually difficult, my long experience working on these taxa and the relative limited theraphosid fauna of Uruguay helped in the recognition. If identification with such methods failed, dissection of immature spermathecae was attempted. When doubts about identification still remained, specimens were eliminated from the study.

Six fields on the patch of urticating hairs (dorsal abdomen) were sampled as suggested by Bertani (1997). Hairs were removed with forceps and placed separately on microscope slides for examination. When only one type of hair was found in this first examination a general sample of urticating hair patch was examined to confirm the first results. To estimate spider size, carapace length (CL) was measured in mm with an ocular micrometer.

RESULTS

The presence of Types I and III urticating hairs in adults of *A. suina* and *E. weijenberghi* is here confirmed as well as the presence of Types III and IV in adults of *G. mollicoma*, *P. longisternale* and females of *H. uruguayense*. In all the species studied, urticating hairs Types I or IV occur early in development, from very small juveniles. Type III urticating hairs occurred later in the development and after the occurrence of the other type present (Figs. 1–5). The minimum size in which Type III hairs occurred was in a relatively wide range in all species: 6.0 mm in *H. uruguayense*, 7.0 mm in *G. mollicoma*, 7.6 mm in *P. longisternale*, 9.3 mm in *E. weijenberghi* and 13.2 mm in *A. suina*. In these two last species, in which adults have Types I and III urticating hairs, Type III is acquired at larger sizes than in the three former species



Figures 1–5.—Size (carapace length) and Types of urticating hairs present in individuals of some theraphosid species. 1. *Acanthoscurria suina*. 2. *Eupalaestrus weijenberghi*. 3. *Grammostola mollicoma*. 4. *Homoeomma uruguayense*. 5. *Plesiopelma longisternale*. (White bars indicate the presence of Type III urticating hairs; black bars indicate the presence of Types III + I in Figs. 1, 2 and the presence of Types III + IV in Figs. 3–5).

having Types III and IV. The minimum size of occurrence of Type III urticating hairs in each species was not correlated with adult (male) size ($r = 0.43$, $P < 0.05$).

In *G. mollicoma*, one medium sized juvenile lacked Type III urticating hairs (Fig. 3); a similar phenomenon was observed in three large juveniles of *H. uruguayense* (Fig. 4). One of these individuals of *H. uruguayense* (7.8 mm) was dissected and had immature spermathecae.

In large individuals with Types I and III urticating hairs present, hairs of intermediate morphology were also found. However, in large individuals with Types III and IV urti-

cating hairs present, hairs of intermediate morphology were not recognized.

At least some Type III hairs in individuals which have Types I + III hairs showed some differences from Type III hairs of individuals having Types III + IV. These differences can be summarized as follows: the proximal end of Type III hairs has a broad axis; with high magnification, this region showed reversed flattened barbs (Fig. 6) in specimens having Types I + III hairs. In specimens with Types III + IV hairs, the proximal end of Type III hairs did not have reversed barbs and the axis was not extended to the tip; lateral diagonal barbs were more extended than the axis of the hair (Fig. 7).

DISCUSSION

Galiano (1969) studied the development of *Grammostola pulchripes* (Simon 1891) and indicated the occurrence of ramified hairs on the dorsal abdomen of spiders in the fifth instar (2.54 mm). These hairs can now be interpreted as Type IV urticating hairs, taking into account that a detailed description was done later by Cooke et al. (1972) and personal observations. Galiano (1973) also indicated the occurrence of Type I urticating hairs in the fourth instar (2.03 mm) of *Acanthoscurria sternalis* Pocock 1903. The present results agree with Galiano (1969, 1973) in the early occurrence of urticating hairs in theraphosids. Although Galiano (1969, 1973) only studied early developmental stages, her results are congruent with the precedence of Type I hairs in *A. sternalis* and the precedence of Type IV hairs in *G. pulchripes*.

Sexual dimorphism was observed in some theraphosid species by Bertani (1997) and Pérez-Miles (2000) in which males have two types of urticating hairs while females have only one (lacking Type III hairs). Considering that Type III hairs are acquired later during development, it seems probable that in these species with sexual dimorphism only males differentially gained Type III hairs during development rather than female losing these hairs. This could explain the results for *H. uruguayense*, in which some large juveniles (one with immature spermathecae) lacked Type III urticating hairs while other slightly smaller juveniles (probably males) acquired Type III urticating hairs. This species show

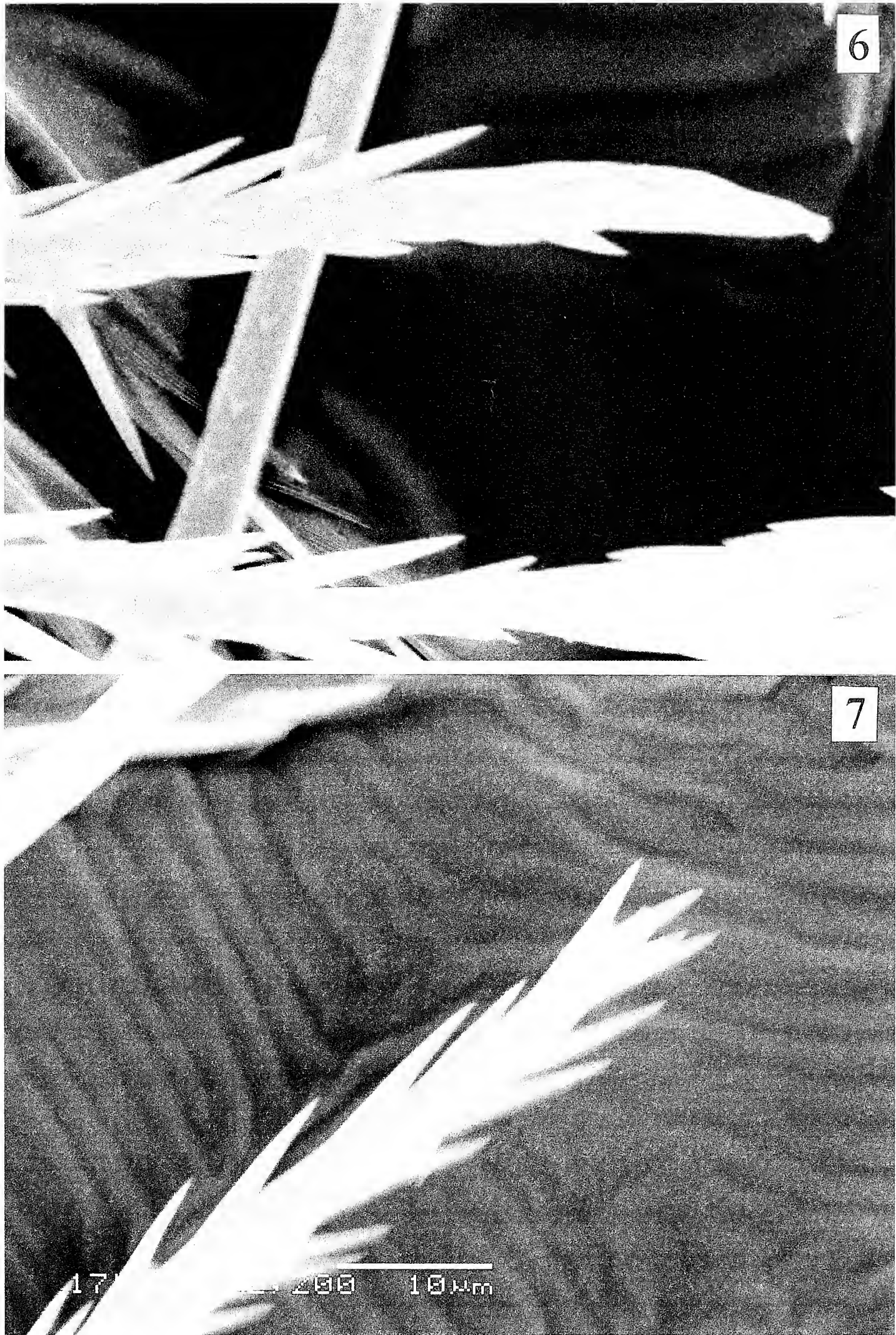
sexual dimorphism in adults: males have Types III + IV while females have only Type IV.

It also seems probable in species without sexual dimorphism that juvenile females acquire the Type III urticating hairs later than males. This could explain the occurrence of some large juveniles of *A. suina* and *G. mollicoma* which lacked Type III urticating hairs.

The co-occurrence of different urticating hair types forced Pérez-Miles et al. (1996) and Pérez-Miles (1992, 2000) to code these types as independent presence/absence characters, since homology among them was not reliable (these characters do not pass the conjunction test). The presence of intermediate hairs between Types I and III and between III and IV were found by Bertani & Guadanucci (1999). Bertani & Guadanucci (1999) proposed serial homology and considered Types I and IV as derived from Type III. Although ontogenetic precedence was seriously contradicted in cladistic analysis (Nelson 1978, 1985; De Queiroz 1985; Kluge 1985; Wheeler 1990), if accepted, present results would conflict with this polarization. But if polarization is inverted another conflict remains: Type III hairs could not be derived from two different states (Type IV and Type I). Another unexpected hypothesis could be considered: that Type III hairs represent two different kinds of non-homologous hairs masked by surface similarity, derived respectively from Types I and IV. Presumably ecological pressures on large spiders of the New World are similar and this fact could explain the convergence to a Type III morphology, probably due to their efficacy for defensive purposes. This hypothesis could be compatible with the homoplasy found for Type III hairs in comparison with the more congruent behavior of Types I and IV in the cladograms of Pérez-Miles et al. (1996) and Pérez-Miles (2000). Also the morphological differences found between some Type III hairs of species also having Type I with respect to species also having Type IV, could support this hypothesis, but further studies are necessary to confirm these preliminary observations.

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Figures 6–7.—SEM photographs showing apical morphology of Type III urticating hairs. 1. *Acanthoscurria suina* (this species also has Type I hairs). 2. *Grammostola mollicoma* (this species also has Type IV hairs).

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LONG-DISTANCE WANDERING AND MATING BY THE DANCING WHITE LADY SPIDER (*LEUCORCHESTRIS ARENICOLA*) (ARANEAE, SPARASSIDAE) ACROSS NAMIB DUNES

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ABSTRACT. Adult males of the Dancing White Lady Spider (*Leucorchestris arenicola*, Araneae, Sparassidae) occurring in the dunes of the Namib Desert, Namibia, frequently wander far out of their 3 m radius territories on dark nights. They move across bare dune slopes in search of mating opportunities and subsequently return to their burrows. In the current study, I describe the long-distance movements and navigational ability of males and examine how their wandering behavior relates to mating and interactions with other males. In 16 observed complete excursions, male spiders walked 51 m (median, range 16–91 m) from their burrow along a path of 134 m (42–314 m). The return path was shorter than the outgoing path, had less than $\frac{1}{2}$ as many turns, and rarely retraced the outgoing path. Typically, the return path across open terrain had a straight section (median 33 m, range 10–89 m) which was directed towards the home burrow with a maximum angle of deviation of 5° . Males crossed 0–5 territories of adult males and as many female territories, mating in about half of the encounters with females. Males avoided each other and signaled with intense sand drumming. Adult males differ in size and there are indications that they compete with each other for mates by long-distance movements, drum-signaling each other, and interfering with mating. During three years of observations of a *L. arenicola* population, 8% of the largest males did 51% of the mating. Spiders of both sexes were promiscuous, and individuals mated with each other on several occasions. The current study prompts future investigations concerning male orientation and its neurophysiological basis, their ability to locate females, as well as the inter- and intrasexual relationships of *L. arenicola*.

Keywords: Navigation, orientation, homing, signaling, mating system

Long distance navigation of animals has long fascinated scientists and the mechanisms of these remarkable capabilities are rarely understood. Spiders have been objects for investigating orientation and navigation and several kinds of mechanisms have been suggested as underlying their homing behavior (Wehner 1992). While some spiders appear to use idiothetic information, mediated by the slit-organ proprioceptors (Seyfarth et al. 1982), others may rely on visual cues, gravity, substrate characteristics, vibrations, or a mixture of several mechanisms (Crawford 1984; Suter 1984; Görner & Claas 1985; Mittelstaedt 1985; Rovner 1991; Dacke et al. 1999; Marshall 1999; Barth 2001). However, these studies were confined to short-distance movements, either on the web, or within several meters of the retreat. This is because spiders usually do not travel far and navigational precision does not appear to be important for

some observed long distance movements, such as ballooning.

The Dancing White Lady Spider, *Leucorchestris arenicola* Lawrence 1962 (syn. *L. kochi* Henschel 1990a; Sparassidae), of the Namib Desert is a wandering spider that regularly walks over bare dune sand at night and returns to its burrow. Immature and female spiders confine these movements to within their foraging territory of ca. 1–3 m radius (Henschel 1994). However, adult males move considerably further, several tens of meters, and return to their original home retreat using behavior other than retracing the outgoing path (Henschel 1990a). The distances exceed the foraging territory by one to two orders of magnitude and in this paper they are referred to as long-distance movements.

Leucorchestris arenicola are so large (2–5 g) that they leave distinct tracks on dry, open, unvegetated sand dunes (Henschel 1987; Birk-

hofer 2000). In the Namib, afternoon winds usually erase previous tracks. The movements of spiders that wandered on calm nights are clearly visible at sunrise, when the shadows of spider footprints are clearly visible. During earlier studies (Henschel 1990a, b, 1994, 1997), spider tracks were compared with observed activities and this makes it possible to interpret tracks, an important component of the current study.

In the current paper, I describe the movements of male *L. arenicola* and compare the characteristics of the outgoing path with the return path in order to examine their navigational ability. Mating opportunities appear to be the motivation for the long-distance movements of *L. arenicola* (see Henschel 1990a). In this paper, I therefore also present first insights into their mating system, mating frequency and male-male competition.

METHODS

Taxonomy.—Lawrence described two species of *Leucorchestris* from Gobabeb. The first was *Leucorchestris arenicola* Lawrence 1962, based on an immature individual, and an adult female in 1966. While Lawrence did not describe a male *L. arenicola*, he named an adult male from Gobabeb, *Leucorchestris kochi* Lawrence 1965. Based on 34 occasions of *L. arenicola* mating with *L. kochi*, Henschel (1990a) suggested that these two are synonymous and that *L. arenicola* is the senior synonym. Despite extensive observations by Henschel (1997) near Gobabeb, no other congeners have been found in this area. The current observations of mating confirm the synonymy, and *L. arenicola* is used throughout this paper. Among 144 voucher specimens of *L. arenicola* from this project deposited in the National Museum of Namibia in Windhoek, 32 are adult females and 21 adult males.

Natural history.—*Leucorchestris arenicola* is endemic to the Great Dune Sea of the Namib Desert (Lawrence 1962, 1965, 1966; Henschel 1990a, 1997). This large, nocturnal sparassid spider, forages primarily on tenebrionid beetles or any other small animal, including conspecifics (Henschel 1990a, 1994). Probably through vibrations of the sand, moving prey are detected up to 3 m away. The preferred microhabitat is the gently sloping portions of dunes. This largest of several sympatric sparassid species appears to exclude

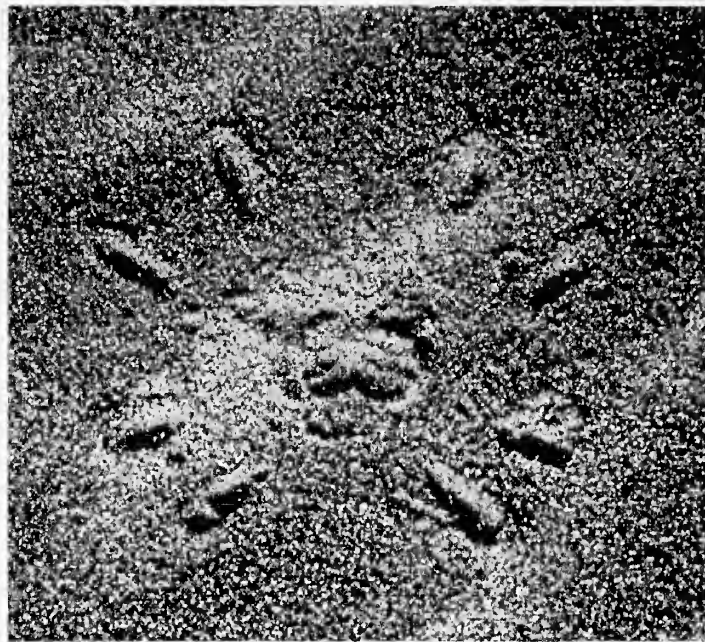


Figure 1.—Drumming spoor of a male spider, showing the eight indentations of the tarsi on the outside, and of the coxae in the middle. The opisthosoma has left a dent behind the coxae, and in front of them are two marks made by the pedipalps, giving the track direction (the spider was facing towards the top of the picture).

other large wandering spiders from this habitat (Henschel 1997). The population density is 9–302 *L. arenicola* ha⁻¹ and neighboring burrows are located approximately 3.9 ± 2.1 m apart at a high-density site (Henschel 1990a).

Both sexes mature at two years of age, and the female continues to live for another 6 months to one year. Females are iteroparous and spend approximately 9 weeks in extended brood care. All reproductive activity is seasonal between September and April, but females and juveniles remain active throughout the year. After maturing, adult males only live for another 6–14 weeks and are absent during winter. Males have longer legs (spanning 10–14 cm) than females (6–9 cm), and they frequently stop during their long wanderings to drum the sand surface with all eight legs and the body, leaving deep impressions (Fig. 1). Wandering activity is reduced during bright nights, particularly for a week on either side of the full moon.

Study Area.—Fieldwork was conducted during late 1986 to late 1989 at Visnara (23°33.835'S; 15°02.201'E), a fenced dune area of 0.75 ha situated 1 km south of Gobabeb in the Great Dune Sea. A grid of 10 × 10 m marked with poles was placed across Visnara, enabling a spatial resolution of 1 m. Other observations were made at dune sites of

the Central Namib across the Great Dune Sea (22°–26°30'S; 14°30'–16°E).

Fieldwork.—All burrows of *L. arenicola* at Visnara were marked with numbered flags and their position in the grid noted. Size, development stage and sex were determined either by capturing and releasing spiders (Henschel 1991), or by looking into the burrow with the aid of an ophthalmic mirror to examine diagnostic features such as epigyna, pedipalps and leg spination (Henschel 1990a). Spiders were individually recognizable by their use of marked burrows, as well as by marking them with a spot of water paint (Plaka) on the dorsal side of the patella. Not all males were measured directly, but spider size is correlated with trapdoor size (carapace width vs. trapdoor diameter: $r^2 = 0.85$; Henschel 1990a), which was measured for all spiders.

Spider activity was recorded from tracks examined after sunrise. The interpretation of tracks was validated with direct observations at night, made by periodically scanning areas with known high densities of spiders using a flashlight from stationary observation points (direct following of spiders disturbs their activity). In this way, tracks left after drumming or mating were identified. All "observations" referred to in the current paper are records of tracks. Burrow entrances were checked on 21,771 occasions during the three study years, with each early-morning check representing an "observation-night" of an individual spider. The data set comprises 1201 observation-nights of 75 adult males and 3175 observation-nights of 103 adult females.

Long distance excursions of males from known burrows were tracked, and their entire paths were drawn onto a 1 m gridded map, i.e. the resolution of movements was 1 m, and smaller deviations were ignored. Linear movements were also recorded simplified (e.g., when a spider walks in a "straight line" the path is actually slightly undulating with deviations < 1 m), but leading in the same general direction. Due to large variability in male size, it was often possible to distinguish drum-marks of different males from each other in cases where they crossed each other.

For the purpose of the current study, a subsample of 25 complete outgoing and return movements of 16 *L. arenicola* males was selected for detailed analysis from a total record of 157 excursions (the total data set includes

many incompletely mapped paths). The 25 paths were digitized, and the following was calculated: total path distance, maximum linear distance from the burrow, outgoing path distance, length of the longest straight section, number of turns, and the number and location of drum-marks. The same data were obtained for the return path as for the outgoing. The target angle was the relative direction of approach towards the burrow of the longest sector on the return path, with 0° being on target (± 1 m based on map cell size); the target accuracy was the distance of the path trajectory from the burrow.

By superimposing the path onto the population map, it was possible to determine the number of territories that a wandering male crossed. Previous tests with protected, released spiders indicated that resident spiders had a territory of about 3 m radius around their burrows (Henschel 1990a). Sometimes direct interactions occurred, such as mating. Probable evidence for other more cryptic interactions were drum-marks left by a male crossing an inactive spider's territory, or two drumming males circling each other at distances of several meters. The distance of the burrows of two females situated closest to the male's burrow along his journey was measured (and if mating occurred, the mated female's distance from the male burrow was recorded).

Data analyses.—Spatial data on male movements were not normally distributed (Kolmogorov-Smirnov Test, $P > 0.05$). To describe wandering behavior, one observation per male ($n = 16$) was selected and 9 further observations were used to examine variation in behavior by individuals. The non-parametric Wilcoxon matched pairs test was applied to compare variables between the outgoing and return paths, as well as interactions towards males compared to females on each journey. Results are given as median, quartiles and range. Sample size (n) of observations of male movements was 16 unless stated otherwise. Observations of mating behavior involved the entire three year data set ($n = 3376$ observations of adults), and a chi-squared test was used to examine whether spider size affects mating frequency.

RESULTS

Movement patterns.—The 16 study males wandered up to 91 m (median 51 m) away

Table 1.—Path analyses for 16 excursions of males, showing the maximum linear distance from the burrow, details of the path, and the accuracy and angle of homing along the longest straight stretch towards the burrow.

Variable	Measure	Median	Quartiles	Range
Linear distance	(m)	51	36–74	16–91
Path distance	total (m)	134	91–231	42–314
Path distance	outgoing (m)	96	47–171	25–213
Path distance	return (m)	39	32–84	16–129
Longest straight stretch	outgoing (m)	20	16–25	6–71
Longest straight stretch	return (m)	33	19–47	10–89
Number of turns	outgoing	11	9–21	4–30
Number of turns	return	2	0–2	0–16
Distance retraced	return (m)	0	0–0	0–13
Angle at burrow	out–return (°)	65	45–98	0–180
Homing	accuracy (m)	0	0–1	0–5
Homing	angle (°)	0	0–2	0–12

from their burrows (Table 1). They often turned, and the median path distance was 134 m (range 42–314 m). The outgoing path was significantly longer than the return path by 146.2% ($P < 0.001$, Fig. 2a). However, the longest straight section was on the return path ($P < 0.05$, median = 33 m). This is because the males made fewer turns on the return path ($P < 0.001$, median = 2 turns) compared to 11 turns on the outgoing path (Table 1). Three times the outgoing path was retraced for 5–13 m. Silken draglines were occasionally produced along the paths (not quantified). Individual males that were observed repeatedly ($n = 9$) moved over different distances (difference from the analyzed observation: median = 73%, range = 1–84%) and did not follow similar paths, although each male returned to the same burrow. The maximum distance recorded for each male in this study was not influenced by spider size ($r^2 = 0.13$, $P = 0.17$).

Homing.—Males usually returned to their burrow from a different direction than the one they took on their outward journey (median deviation = 65°). In all 12 cases where there was no obstruction along the way, the longest stretch of return aimed $< 5^\circ$ towards the burrow, usually being 0°, i.e., going straight towards the burrow (Table 1). Males took the shortest distance back. In the remaining 4 cases, there was a !nara bush (*Acanthosicyos horridus* Cucurbitaceae) or *Acacia* tree in the way, and the returning male walked around the periphery of the obstruction. He deviated 11–31° from the shortest route, and then

turned towards the burrow when the way was clear. On exceptional occasions when a male missed his burrow, his subsequent movement behavior changed (e.g., Fig. 2b). He made frequent turns and loops, and steadily moved closer to his own territory until he found the burrow. There is no record of a male not finding his burrow. Only one male constructed a new burrow several meters away from his original burrow upon returning to his territory.

Encounters.—The *L. arenicola* population at Visnara was quite densely packed, so that as soon as males moved out of their own territory (3 m radius), they crossed 2–35 territories of other known spiders at Visnara (Table 2). There were no differences in the number of adult males and adult females encountered by wandering males (quartiles: 1–2; $P > 0.05$). The closest territory of an adult female that they crossed was a median distance of 15 m (range 4–64 m) from the wandering males’ home burrow, and the second female was 55 m (28–89) away. During one excursion, the wandering male did not encounter a female, even though a female burrow was 16 m from his burrow, and this male moved 74 m further than the distance to the closest female. In six (40%) of the 15 excursions where a female was encountered, this was not the closest female to the male’s burrow. Five of these males did locate the closest female during other excursions. The 16 males encountered females on 22 occasions, and mated on 15 (68%) of the encounters (when examining all 25 excursions, the proportion

was 57%). Two of the males mated twice during one night's excursion.

Drumming.—Drumming (Fig. 1) was frequently performed on the outgoing journey (median 17, range 0–54 times), compared to rare instances of drumming on the return (upper quartile = 0, maximum = 15; $P < 0.001$; Table 2). For 71% of the drumming incidents, it was possible to ascertain a likely relationship to other adult *L. arenicola*, as either another male responded in kind, or the drumming occurred near the burrow of an adult spider. Drumming by wandering males occurred near another male significantly more often (95% of 239) than drumming near females (5%, $\chi^2 = 124$, $df = 2$, $P < 0.001$, Table 2). On six occasions when a wandering male walked over the territory of an inactive adult male, the wandering male drummed.

When two wandering males approached each other ($n = 10$), they avoided one another by several meters in eight cases and in two cases circled each other closer than 1 m (but the males apparently did not contact each other). Some of the most complex movements by males across the study area were when two males maneuvered around each other across a wide field (Fig. 2c). In the case shown on Fig. 2c and in a second case, it appeared that mating had been interrupted by the arrival of a second male.

Mating.—Data on mating were obtained in the course of 3376 observations of 178 adult spiders (75 males) at Visnara over three years. Six males performed 51% of 63 copulations recorded in the course of three years, while 24 males did the remainder. Excursions in which mating occurred were usually followed by one or more nights of inactivity. However, on six occasions (9.5%), males mated on successive nights. For 45 males, no mating was recorded in 469 observations. Mating frequency significantly increased with male size (Table 3; $\chi^2 = 8.1$, $df = 2$, $n = 30$, $P < 0.05$). The six males with the highest mating frequency were from the middle and largest size classes.

An individual male (#82) was observed for 38 nights over an 11-week period. He undertook 12 excursions (3 of which are part of the mapped data set) and mated ten times with six different females, two of them twice and one three times (Fig. 3). On three excursions he apparently mated twice. Observations of him began soon after full moon, and his initial ex-

cursions were relatively short (< 20 m). However, after a fortnight, at new moon, he wandered farther (Fig. 3).

In 3175 observation-nights of 103 individual adult females, they mated on 55 occasions. Eight females (8%) performed 54.5% of the copulations, and 19 the rest, while mating was not observed for 76 females. This distribution was significantly skewed ($\chi^2 = 0.49$; $n = 103$; $P > 0.05$). On different nights, individual females mated with up to four different individual males. On six occasions (10.9%), females mated on successive nights. During the 6 month seasons, six females mated at least thrice, one four times and one eight times. The latter female mated with the same male on four successive nights. During a five month observation period, she again mated with this male as well as two other males, once with different males on two successive nights. On four other occasions, a female mated a previous partner. On many occasions when a male crossed a female territory, mating did not take place (43% during all 25 mapped excursions). Small females mated less frequently than large females (Table 3; $\chi^2 = 7.8$, $df = 2$, $n = 27$, $P < 0.05$).

During 1201 observation-nights of 75 individual adult males at Visnara during the course of three years, males wandered out of their territories on 157 (13.1%) occasions, mainly between the months of October to February (Fig. 4). Given a median natural longevity of 9 weeks after maturation (two new moons), it is calculated from the above that an adult male, on average, wanders 8.2 times during this period, or on 26.0% of the nights of low moon. Thus, a male may expect to mate 4.7 times during his life on average.

Females mated during 1.7% ($n = 55$) of the observations ($n = 3175$). It is thus calculated that during a season, an average female mates 12.1 times per 8 month breeding season, or 10.1% of the low-moon nights. Given that the sex ratio is female-biased (males: females = 0.38: 1; see also Henschel 1990a), this estimate of females mating corresponds roughly with that calculated from the frequency of males mating ($26.1\% \times 0.38 = 9.9\%$).

Mortality.—It was difficult to assess the risk of long distance movements. All males suddenly disappeared for unknown reasons. In six cases, wandering males were captured by predatory gerbils, representing 3.8% mortality

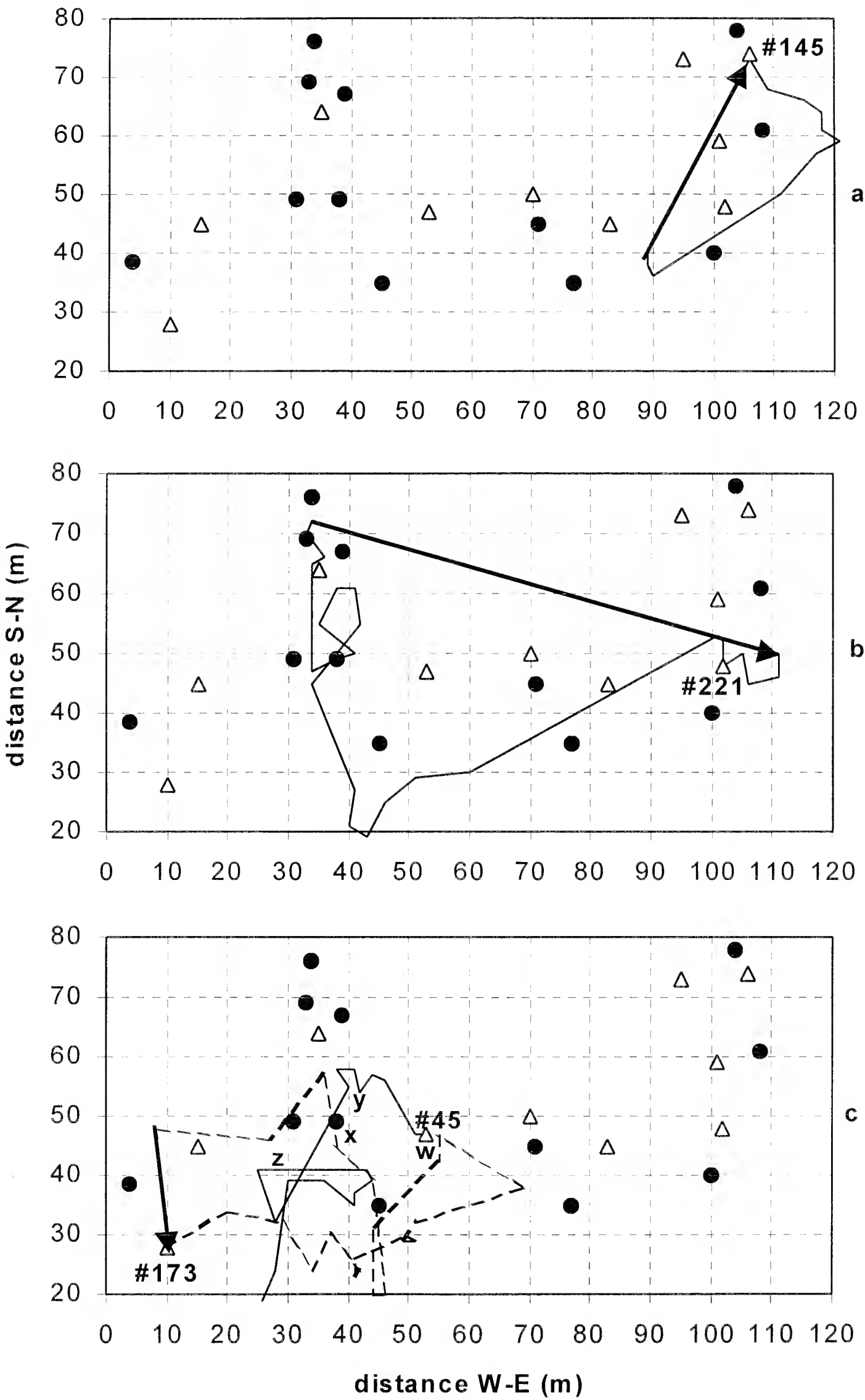


Table 2.—Number of territories crossed, encounters and drumming behavior by males during 16 excursions.

Variable	Description	Median	Quartiles	Range	n
Number of territories	all	16	7–23	2–35	16
	adult males	2	1–2	0–6	16
	adult females	1	1–2	0–5	16
Distance (m) to female	closest from burrow	10	7–15	4–35	16
	1 st encounter	15	10–34	4–64	15
	2 nd encounter	55	38–68	28–89	7
	diff. closest–1 st	0	0–13	0–56	15
Drum-marks	outgoing	17	7–21	0–54	15
	returning	0	0–0	0–15	16
	near male	3	0–19	0–48	15
	near female	0	0–1	0–4	15

rate during excursions. Three other males died of unknown cause in their burrows. The fate of the remaining 66 other males was unknown.

DISCUSSION

A main feature of the long distance excursions by the *L. arenicola* males was their unerring return journey to their burrow. Even after long and complex outward excursions with many turns and loops, homing behavior indicated that the wanderers knew where their burrows were and returned by the shortest possible route, even when moving around obstacles. A male changed his behavior to a meandering search when he missed his burrow after a long journey.

The need to return to the home nest rather than building a new nest may be a question of the energy required to construct a new burrow (Henschel & Lubin 1992), as well as

avoidance of risk of exposure to predators including conspecifics during burrow-making (Henschel 1997). Males always returned to their existing burrow, but in one case the male walked on after returning to his burrow and dug a new burrow nearby. Of 36 burrows of adult males that I excavated and more than 100 more that I examined in the Namib dunes elsewhere than at Visnara, only three had been dug during the previous night, as indicated by a burrow length of less than 15 cm, scrape-marks around entrance closed with silk curtain instead of trapdoor. This indicates that males seldom establish new burrows.

Mating System.—Excursions need to be long to encounter females. Even when walking over 130 m, males crossed territories of only 1–2 adult females. Many females did not mate when males crossed their territory, but such females did sometimes mate on other encounters. This may indicate that females do

←

Figure 2.—Movements of males illustrated on a 10 × 10 m gridded map of the study area at Visnara. The locations of some burrows of *L. arenicola* adults (closed circle = female, open triangles = male) are shown. The areas devoid of burrows in the upper middle and upper left are vegetated, the remainder bare sand. Lines depict movements of four males from the burrows labelled #. Bold arrows are the longest stretches on the return journey. (a) A typical 103-m long journey of the male #145 on 26 December 1986 is shown, with several turns when going outward and a direct return journey. (b) This general pattern is also evident for #221 on 23 February 1987, but in this case there was an 80 m long return path and the male missed his burrow by 4 m, then turned and made several loops before finding his burrow. (c) On 27 February 1987 males #45 and #173 wandered simultaneously. w: #173 moved towards #45 and the two males closely circled each other at the burrow of #45 with much drumming; x: #173 mated; y: #45 drummed and circled some 5 m from x. The two males crossed each other's tracks at x, possibly interrupting mating. z: The two males walked parallel 5–10 m apart and both drummed at short intervals, with #45 following this up by making loops several meters from the female. After that #173 returns to his burrow, and #45 makes a long excursion (total 314 m, not completely shown here) before returning home.

Table 3.—Mating frequency by males and females of three size classes, as indicated by trapdoor diameter and mass.

Trapdoor Diameter (mm)	Mass (g)	Males		Females	
		Observation -nights	Mating %	Observation -nights	Mating %
<21	<1.6	376	3.7	692	0.9
21–23	1.6–2.1	436	5.0	1029	1.3
>23	>2.1	348	7.8	1363	2.4

not mate throughout their reproductive cycle. Many females, however, did not mate at all, and this was particularly true for small females, perhaps because they are less fecund. In both sexes, a few individuals mated more often than others. The most successful individuals were of large to medium size. Successful males undertook excursions every 1–4 nights and could mate twice per excursion. Both sexes mate multiple times and individuals can mate several times with each other as well as with other individuals, i.e. the current study demonstrates that both sexes are promiscuous. Relationships between the sexes are likely to influence the home range of an adult male, and this therefore warrants further study in order to understand male movements.

Although males avoided direct encounters, wandering males did approach territories of other males and signaled by drumming. *Leucorchestris* males drummed in the vicinity of other males, even if the latter were inactive (at least had not left their burrows), and seldom drummed near females. By contrast, drumming appears to be an important courting signal in another sparassid, *Heteropoda venatoria* Thorell 1878 (Rovner 1980). Drum-

ming by *L. arenicola* towards a male may cause a rival to withdraw or keep out of the way of the signaler and can perhaps interrupt mating, as suggested by two cases. Differences in male size (1.0–2.8 g) are likely to affect such male-male competition. Besides evidence that most drumming by *L. arenicola* appears to be an intrasexual signal, the above conclusions on male-male relationships are tentative and require verification.

Navigation.—The mechanism that males use for navigation is unknown. Such precise orientation over long distances suggests either highly developed path integration (using egocentric information), or orientation in the landscape (geocentric information). The two different sets of information could be coupled, as they are in ants (Wehner & Wehner 1990; Wehner et al. 1996). There is currently no evidence for path integration by *L. arenicola*, except perhaps the knowledge of direction and distance to a burrow, demonstrated by the change in behavior when a male passed his home burrow by mistake after a long or complex journey. If path integration is involved, the complex case of Namib dune sparassids warrants further study.

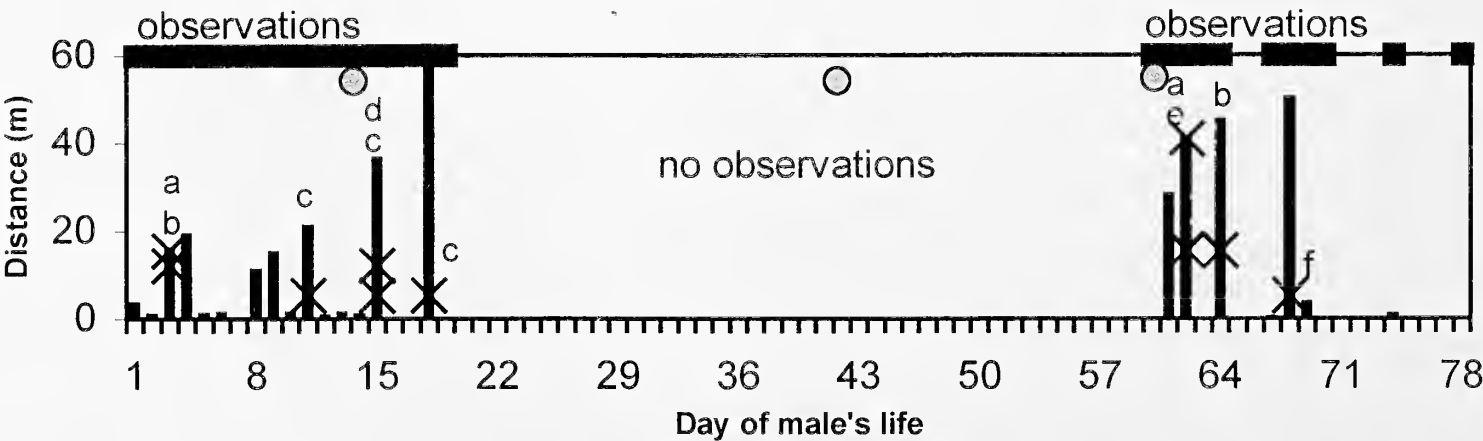


Figure 3.—Observations for 38 days during 78 days of adult life of marked male #82 from one burrow between 19 December 1986 and 6 March 1987. Days of observation are indicated at the top. Bars show the linear distance (m) that the male moved from his burrow in a night. 'X' indicates the distance of mating with six females a-f. Shaded circles represent new moon.

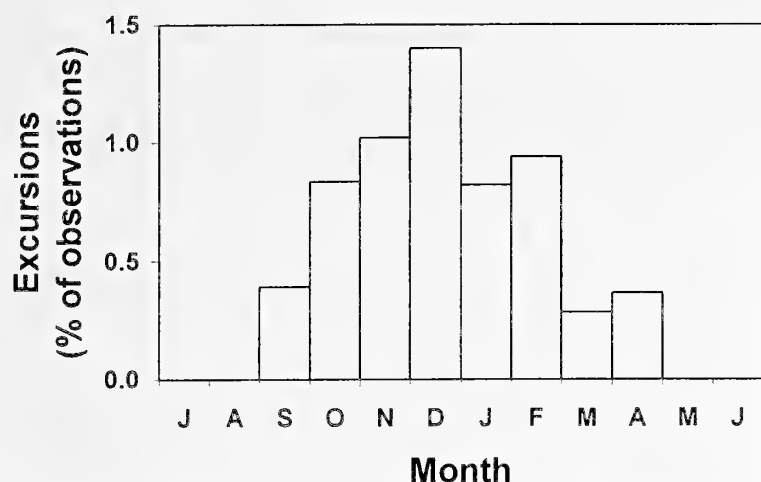


Figure 4.—Observations of male excursions in various months of the austral year, expressed as percent of observations of all spiders during each month (total $n = 21,771$).

For a nocturnal animal of this size, several senses could be important for orientation in the landscape. The eyes, albeit small, may be quite sensitive to light, but the spiders prefer dark to bright nights (Henschel 1990a), probably to avoid risk of predation from visually-hunting predators such as gerbils and nocturnal birds (e.g., owls). Olfaction is another possible sensory mechanism, as has been demonstrated for other sparassids (Rovner 1980; Rowell & Avilés 1995). Pompilid wasps can follow the tracks of *L. arenicola* (pers.obs.) and wheel spiders *Carparachne aureoflava* Lawrence 1966 (Henschel 1990b), suggesting that the spiders leave olfactory traces, perhaps in silken drag-lines (Schulz & Toft 1993). Drumming by *L. arenicola* males indicates that they can detect the territories of inactive males, perhaps by smell. Trichobothria enable spiders and scorpions to detect wind direction, facilitating anemotaxis (Linsenmair 1968; Barth et al. 1995). It is possible that *L. arenicola* makes use of the fairly predictable patterns of summer winds in the Namib (Tyson & Seely 1980).

Many psammophilous animals detect vibrations transmitted through sand over distances of centimeters (Brownell 2001) to meters (Narins et al. 1997). Sand is a particularly good conductor of compressional and Rayleigh waves originating from the movement of animals on or in sand (Brownell 1977). Vibrations enable small animals to detect moving insects (Brownell 1977, 2001; Narins et al. 1997; Enders et al. 1998) or wind-blown sand (Hanrahan & Kirchner 1994). Many spiders are well endowed with vibration sensors

(Barth 2001). *Leucorchestris arenicola* appear to be highly sensitive at detecting vibrations, e.g., directional interception of territorial intruders or prey over 1–3 m, apparent maneuvering of two drumming males around each other at distances of several meters. It is possible that detection of vibrations assists *L. arenicola* in navigation.

Elucidating the mechanisms of orientation and navigation of *L. arenicola* is a challenge for future studies. The sensory environment is quite different from that of other case studies. Further studies of the Dancing White Lady Spider could therefore make important contributions to the understanding of navigation on the whole, and could find applications such as broadening the scope of navigational robotics (Lambrinos et al. 1997; Wallander & Russell 2001).

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SPIDER ASSEMBLAGE STRUCTURE AND STABILITY IN A HETEROGENEOUS COASTAL DUNE SYSTEM (BELGIUM)

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ABSTRACT. An analysis of the spider assemblage structure and the presence of indicator species in the Flemish coastal dunes are presented. The analysis is based on data from more than 170 year-round pitfall sampling campaigns from the 1970s onwards. We were able to find indicator species for all identified habitats. The assemblages are determined by variation in vegetation structure (succession), atmospheric and soil humidity and the occurrence of both natural or anthropogenic disturbance. In the fragmented habitats (grasslands and grey dunes), a clear relationship was found between the mean habitat size and the stability of the assemblage composition. In moss dominated dunes and short grasslands total species numbers do not increase with patch size. Due to microhabitat variation and the possibility of attaining viable population sizes the total number of typical species is, however, higher in larger patches. In small patches, edge effects are more important and the number of observed species is enlarged by the intrusion of species from nearby habitats.

Keywords: Araneae, indicator species, habitat size, species-area relationship

Coastal dunes in Europe have been the subject of several spider community studies which reveal that the species composition is characterized by the presence of many rare and threatened species. Especially in northern (Almquist 1973) and western Europe (Duffey 1968; Bell et al. 1998), such investigations have been carried out. Carabid beetles (Desender et al. 1992; Desender 1996) and dipteran flies (Pollet & Grootaert, 1996) were also studied in the Belgian coastal dunes. Such studies are necessary for the assessment of the conservation value of these habitats. General assemblage descriptions together with more detailed knowledge of landscape-level ecological relationships such as multi-habitat use (Bonte et al. 2000a), colonization abilities (Bonte et al. 1998), population genetics (Desender et al. 1998) and population dynamics (Desender 1996; Baert & Desender 1993) should be taken into account when developing a nature conservation policy.

Since the beginning of the 20th century the total area of coastal dunes that have not been

built upon in Belgium diminished from approximately 6000 ha to less than 3800 ha (Vermeersch 1986). The remaining dune areas are characterized by an overall increase of competitive plant species like Sea Buckthorn *Hippophae rhamnoides*, Burnet Rose *Rosa pimpinellifolia* and Wood Small Reed *Calamagrostis epigejos*, due to the retreat of local dune farmers after World War II and a decrease in the rabbit population due to myxomatosis and other diseases. This shrub and grass encroachment is possibly triggered by atmospheric N-deposition and enhanced by positive feedbacks in the nitrogen cycle (Veer 1997) and by the increase of nitrogen-fixing Sea Buckthorn. The soil nitrogen and mineral content will influence the trophic status of the vegetation, which is strongly related to the amount of organic components in the upper soil layer (Krabbenborg et al. 1983). Current habitat management is directed to the conservation and restoration of wet, herbaceous grasslands in dune valleys and stable meso-

Table 1.—Characterization and total number of pitfall-data from the sampled dune habitats.

Type	Indicative plant species	Number of pitfall-traps
Dune woodland	Trees: <i>Alnus glutinosa</i> , <i>Acer pseudoplatanus</i>	3
High, woody shrubs	Shrubs: <i>Crataegus monogyna</i> , <i>Hippophae rhamnoides</i>	13
Thick humid <i>Calamagrostis</i> grassland	Grass: <i>Calamagrostis epigejos</i>	20
Vital humid Sea-buckthorn-Liguster shrubs	Shrubs: <i>Hippophae rhamnoides</i> , <i>Salix repens</i> , <i>Ligustrum vulgare</i>	10
Wet eutrophic open dune valleys	Sedges and grasses: <i>Juncus subnodulosus</i> , <i>Carex riparia</i> , <i>Iris pseudacorus</i>	6
Thick dry <i>Arrhenaterium</i> grassland	Grasses: <i>Arrhenatherium elatius</i> , <i>Avenula pubescens</i>	13
Dry Sea buckthorn shrub (in grassland mosaics)	Shrub: <i>Hippophae rhamnoides</i>	6
Dwarf shrubs	Dwarf-shrub: <i>Rosa pimpinellifolia</i>	18
Wet mesotrophic open dune valleys	Sedges and grasses: <i>Juncus subnodulosus</i> , <i>Carex trinervis</i> , <i>C. flacca</i>	12
Short grazed mesophytic grasslands	Grasses and herbs: <i>Luzula campestris</i> , <i>Galium verum</i> , <i>Avenula pubescens</i> , <i>Koeleria albescens</i>	15
Wet oligotrophic dune valleys	Grasses and sedges: <i>Juncus articulatus</i> , <i>Carex trinervis</i>	10
Marram dunes	Grass: <i>Ammophila arenaria</i>	9
Moss dominated dry oligotrophic dunes (Grey dunes)	Mosses, annual herbs and grasses: <i>Tortula ruralis ruraliformis</i> , <i>Aira praecox</i> , <i>Erodium cicutarium</i> , <i>Corynephorus canescens</i>	29
Bare sand dunes	Grass: <i>Festuca rubra arenaria</i>	9
Anthropogenic distributed sand dunes	Herb: <i>Cirsium arvense</i>	5

phytic grasslands through large-scale removal of shrub, followed by horse and cattle grazing.

In order to develop tools for future monitoring we: 1. investigate which parameters influence the variation in species composition and 2. determine indicator spider species for all of the dune habitats occurring along our coast; and since a crucial question in habitat restoration is the effect of patch area on the presence of typical species (stenotopic species) we also 3. investigate the species-area relationships for two highly fragmented habitat types.

METHODS

Data collection.—The total assemblage analysis is based on data from 178 pitfalls, which were operative during an entire year-cycle in all kinds of dune habitats of the Belgian coastal dunes from the 1970s onwards (Hublé 1975; Hublé 1976; Van Biervliet 1978; Hublé & Maelfait 1981; Baert & Desender 1993; Maelfait 1993; Bonte & Hendrickx 1997; Bonte et al. 1999; Baert et al. unpub. data). In each sampling station three to five

traps were placed with a distance of 5–10 meter between each pitfall (the traps are glass jam jars with a diameter of 9.5 cm, filled with a 10% formaline solution). In total more than 65,000 adult spiders were identified, resulting in data on the occurrence of 214 species. Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences in Brussels. Of these, 159 species were represented by more than five individuals caught and can thus be considered resident species and not rare vagrants (cf. Maelfait & Baert 1988). The sampled vegetation types, the dominant plant species and the number of pitfall traps used are listed in Table 1.

Community structure and Indicator species.—The community-structure is indirectly determined via Detrended Correspondence Analysis (Hill 1979a) with the data from the separate pitfalls. Only the more abundant species were taken into account for the ordination analysis. This methodology reveals a multi-dimensional ordering of the samples (here traps) based on their species composition sim-

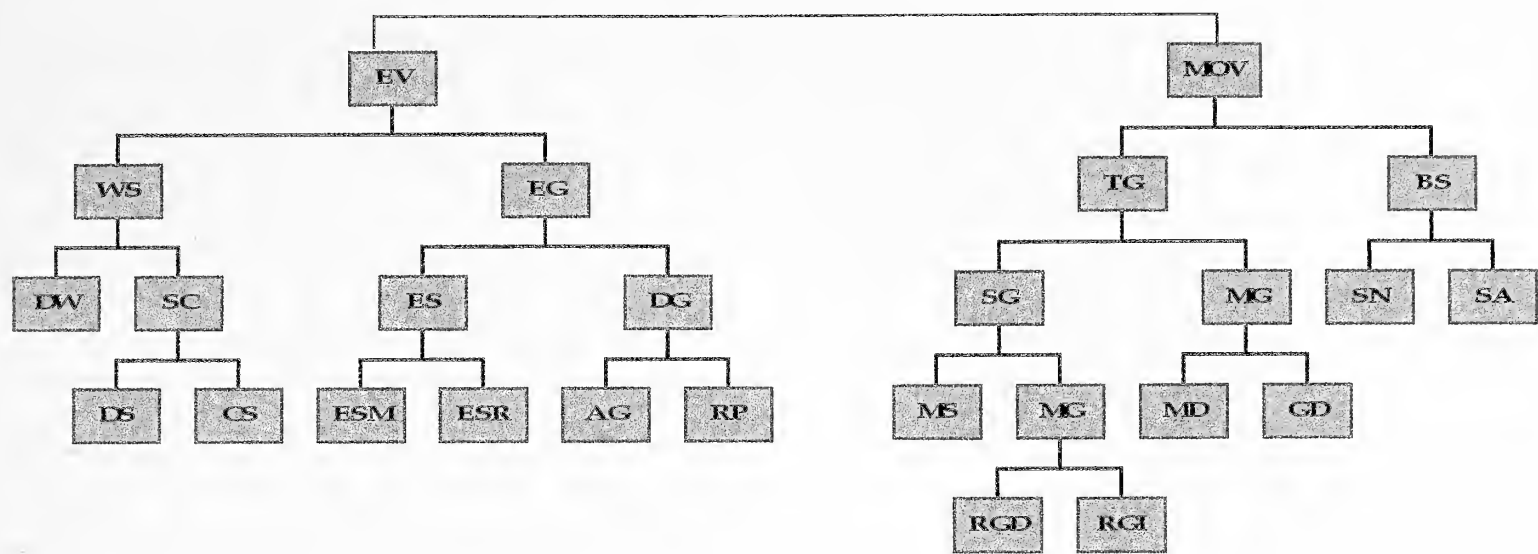


Figure 1.—Dichotomous TWINSpan clustering of the spider composition based on the species presence/absence data. (For abbreviations of the assemblages see Table 2).

ilarity in which traps with a similar assemblage are ordered closely together, while those with a completely different species composition are positioned far apart. Since habitat characteristics were never studied in a standardized way during the several sampling campaigns, only the habitat type and the linked biotic and abiotic variables were indirectly used for the analysis of the parameters structuring the spider assemblage. Data on the stage of vegetation succession, depth of the groundwater level and different kinds of disturbance were taken from Provoost & Hoffmann (1996). Different kinds of disturbance result from natural eolic dynamics (sand overflowing) and anthropogenic factors due to different intensive nature management techniques like mowing of the vegetation (once or twice a year) and grazing (year-round) for the conservation of oligo- and mesotrophic pastures.

We used a TWINSpan-clustering (Hill 1979b) for the determination of the different levels of assemblage similarity, based on the species composition from each pitfall trap. In this way a hierarchical ordering is obtained in which samples are dichotomously separated at different levels. The separation at the first level splits the samples in two different and large groups with common species. The samples from both groups are then again separated based on differences in their species composition. The total dataset is in this way dichotomously clustered at five levels in which the highest levels represent the most detailed sample separation.

Indicator species for all groups at the dif-

ferent levels from the TWINSpan-classification were determined with the IndVal-method (Dufrêne & Legendre 1997). With this methodology, an indicator value is calculated for a species in each cluster group. The indicator value is calculated as: $IndVal_{ij} = A_{ij} * B_{ij} * 100$, where $A_{ij} = N\ individual_{ij} / N\ individual_i$ and $B_{ij} = N\ trap_{ij} / N\ sites_j$. In this formula A_{ij} is a measure of group specificity, where $N\ individual_{ij}$ is the mean number of individuals of species i across traps of group j and $N\ individual_i$ is the sum of the mean numbers of individuals of species i over all groups at that level. B_{ij} is a measure of fidelity, where $N\ trap_{ij}$ is the number of traps in group j where species i is present, while $N\ sites_j$ is the total number of traps in that group. A_{ij} is maximum when species i is only present in group j , while B_{ij} is maximum when species i is present in all traps of the group j . A random reallocation procedure of traps among groups is used to test the significance of IndVal (500 permutations). This index (IndVal) is thus maximal when all individuals of a species are found in a single group of traps and when the species occurs in all traps of the group. As a consequence the maximal indicator value can be interpreted as a measure for habitat specificity.

Because pitfall data record (species specific) activities instead of absolute densities, we only analyzed our data by presence/absence in the ordination, clustering and IndVal calculation. In this way, bias to different climatic conditions between years are eliminated.

Assemblage stability and species-area relationships.—The mean Euclidean distance

between the different axes-scores for pitfalls from the same assemblage, as derived from the multi-dimensional DCA-ordination, was used as a measure for the assemblage instability. Low Euclidean distances characterize traps that sampled analogue species composition, while traps with a completely different species composition have a high Euclidean distance (are ordered distantly). This distance measure is thus an indication for the species composition similarity between traps from the same assemblage. High similarities result thus in low distances and indicate stable species assemblages.

Due to shrub and grass encroachment, mesophytic short grasslands and humid valley habitats became fragmented and diminished in area. A decrease in the area can influence the assemblage structure: especially for small habitat patches, the assemblage stability is expected to decrease because of the extinction of species and the presence of species from adjacent habitats. Therefore, we related the habitat (in)stability to the average area of the different fragmented habitat types as derived from digitized vegetation maps (Provoost & Bonte, unpub. data). Differences in stability between assemblage groups were assessed with Analysis of Variance and related to habitat areas with Spearman rank correlations.

For moss dominated dunes and short mesophytic grasslands (for which we have exact data on the area of the sampled patch), we also determined the relation between the total number of species and the number of indicator species, trapped in three pitfalls, and the area of the sampled grassland patch. The species number-area relationship was analyzed by Pearson correlations between the total number of species and between the number of indicator species and the area of the sampled habitat patch, separately for moss dominated dunes and short dune grasslands.

RESULTS

Assemblage structure.—A total of 15 spider species assemblages were characterized by the TWINSpan clustering. The first division clearly separates the eutrophic vegetations from the meso- and oligotrophic, short grazed habitats. The eutrophic assemblages are separated at the lowest level in dune woodlands, shrubs, marshland and dense grasslands. The mesotrophic and oligotrophic habitats are sep-

arated within the second group (Fig. 1) in short, rabbit-grazed grasslands, mown mesotrophic dune valleys, moss dominated dunes, dynamic Marram-grass (*Ammophila arenaria*) dominated dunes and bare dunes. Significant indicator species per cluster group (Monte Carlo permutations; 500 runs) and their indicator value are listed in Table 2.

The ordination-analysis clearly shows the assemblage structure along three relevant axes. The first axis (eigenvalue 0.689) separates the different samples along a vegetation structure-gradient, where dune woodlands are plotted on the left, bare sandy habitats on the right. The second axis (eigenvalue 0.587) separates the humid from the dry habitats: dune valley vegetations (dune slacks) and Marram dunes above and moss dominated dunes (grey dunes) below (Fig. 2). Interesting is the higher position along the second axis of Marram dunes near the seaside in comparison with those along the inner dune front. This stresses the importance of atmospheric humidity in addition to soil humidity as the second important assemblage structuring parameter. The third relevant axis (eigenvalue 0.383; Fig. 2) is associated with natural (wind in Marram dunes, inundations in dune slacks) and anthropogenic dynamics (especially habitat management: mowing & grazing in short grazed pastures and dune slack meadows); all these disturbed habitats which are indeed ordered at the lower part of the ordination axis.

Stability of assemblages from oligo- and mesotrophic habitats and species-area relationships.—The assemblage stability differs between the different distinguished spider assemblages from oligo- and mesotrophic habitats (Bare sand (BS), mown eutrophic valleys (ESM), Moss dominated dunes (GD), Marram dunes (MD), Mesophytic dune slacks (MS), Dry mesotrophic grasslands (RGD) and inundating mesotrophic grasslands (RGI) (one way-ANOVA, $F_{1,6} = 11.403$, $P < 0.001$). The stability is significantly different between the assemblage groups BS, ESM, GD, MD and the assemblages of MS, RGI, RGD, but does not differ within the two groups. Correlation with average patch size is nearly significant (Spearman $R = -0.750$, $P = 0.052$) and indicates that assemblages from small habitats tend to be more diverse in species composition.

The species-area relationship of the total

Table 2.—Indicator species (Monte Carlo permutations, $P < 0.01$) and indicator value (IndVal) at the different cluster levels (See Fig. 1), with description of the assemblage habitat characteristics.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Eutrophic vegetation (EV) Higher, litter rich, dense Dry or humid	<i>Alopecosa pulverulenta</i> (Clerck, 1757) (Lycosidae)	74.97
	<i>Bathypantes parvulus</i> (Westring, 1851) (Linyphiidae)	51.04
	<i>Centromerus prudens</i> (O.P.-Cambridge, 1873) (Linyphiidae)	60.06
	<i>Centromerus sylvaticus</i> (Blackwall, 1841) (Linyphiidae)	87.08
	<i>Clubiona comta</i> C.L. Koch, 1839 (Clubionidae)	23.60
	<i>Clubiona lutescens</i> Westring, 1851 (Clubionidae)	25.71
	<i>Episinus angulatus</i> (Blackwall, 1836) (Theridiidae)	16.85
	<i>Ero furcata</i> (Villers, 1789) (Mimetidae)	47.03
	<i>Euryopus flavomaculata</i> (C.L. Koch, 1836) (Theridiidae)	49.49
	<i>Floronia bucculenta</i> (Clerck, 1757) (Linyphiidae)	27.77
	<i>Gonatium rubens</i> (Blackwall, 1833) (Linyphiidae)	69.57
	<i>Linyphia triangularis</i> (Clerck, 1757) (Linyphiidae)	12.94
	<i>Maso sundevalli</i> (Westring, 1851) (Linyphiidae)	43.76
	<i>Meioneta saxatilis</i> (Blackwall, 1844) (Linyphiidae)	46.09
	<i>Neriene clathrata</i> (Sundevall, 1830) (Linyphiidae)	25.97
	<i>Ozyptila simplex</i> (O.P.-Cambridge, 1862) (Thomisidae)	71.09
	<i>Palliduphantes ericaeus</i> (Blackwall, 1853) (Linyphiidae)	19.97
	<i>Palliduphantes pallidus</i> (O.P.-Cambridge, 1871) (Linyphiidae)	69.56
	<i>Pirata hygrophillus</i> Thorell, 1872 (Lycosidae)	49.16
	<i>Pocadicnemis juncea</i> Locket & Millidge, 1953 (Linyphiidae)	59.63
	<i>Robertus lividus</i> (Blackwall, 1836) (Theridiidae)	74.39
	<i>Theridion bimaculatum</i> (Linnaeus, 1758) (Theridiidae)	33.35
	<i>Trochosa terricola</i> Thorell, 1856 (Lycosidae)	88.01
	<i>Walckenaeria acuminata</i> Blackwall, 1833 (Linyphiidae)	47.11
	<i>Walckenaeria atrotibialis</i> (O.P.-Cambridge, 1878) (Linyphiidae)	93.17
	<i>Zora spinimana</i> (Sundevall, 1833) (Zoridae)	66.94
Meso-oligotrophic vegetation (MOV) Short, sparse vegetation Rabbit grazed Dry or humid Sandy patches	<i>Arctosa perita</i> (Latreille, 1799) (Lycosidae)	63.24
	<i>Haplodrassus dalmatensis</i> (L. Koch, 1866) (Gnaphosidae)	73.01
	<i>Meioneta rurestris</i> (C.L. Koch, 1836) (Linyphiidae)	34.49

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Woodland and woody shrubs (WS) High vegetation and litter rich Presence of trees (<i>Crataegus monogyna</i>) Dense grasslands (EG) Dense and tall grass layer Litter-rich Dry or humid	<i>Parapelecopsis nemoralis</i> (O.P.-Cambridge, 1884) (Linyphiidae)	53.85
	<i>Styloctetor romanus</i> (O.P.-Cambridge, 1872) (Linyphiidae)	37.22
	<i>Tegenaria agrestis</i> (Walckenaer, 1802) (Agelenidae)	24.72
	<i>Xysticus sabulosus</i> (Hahn, 1832) (Thomisidae)	40.28
	<i>Tapinopa longidens</i> (Wider, 1834) (Linyphiidae)	19.35
	<i>Walckenaeria nudipalpis</i> (Westring, 1851) (Linyphiidae)	44.13
	<i>Clubiona diversa</i> O.P.-Cambridge, 1862 (Clubionidae)	8.09
	<i>Cnephalocotes obscurus</i> (Blackwall, 1834) (Linyphiidae)	35.07
	<i>Enoplognatha thoracica</i> (Hahn, 1833) (Theridiidae)	30.89
	<i>Ero cambridgei</i> Kulczynski, 1911 (Minetidae)	11.53
Thermophilious grasslands (TG) Short, no or scarce litter Dry or humid Dynamics: wind, grazing or mowing	<i>Pachygnatha degeeri</i> Sundevall, 1830 (Tetragnathidae)	71.92
	<i>Pisaura mirabilis</i> (Clerck, 1757) (Pisauridae)	18.92
	<i>Walckenanaeria antica</i> (Wider, 1834) (Linyphiidae)	41.61
	<i>Agroeca lusatica</i> (L. Koch, 1875) (Liocraniidae)	37.57
	<i>Alopecosa barbipes</i> (Sundevall, 1833) (Lycosidae)	34.59
	<i>Bolyphantes luteolus</i> (Blackwall, 1833) (Linyphiidae)	16.00
	<i>Centromerita concinna</i> (Thorell, 1875) (Linyphiidae)	62.25
	<i>Walckenaeria monoceros</i> (Wider, 1834) (Linyphiidae)	32.82
	<i>Xysticus kochi</i> Thorell 1872 (Thomisidae)	64.91
	<i>Erigone longipalpis</i> (Sundevall, 1830) (Linyphiidae)	57.14
Bare sand (BS) No vegetation Dune woodland (DW) Dominance of trees (<i>Alnus glutinosa</i>) Litter-rich Humid	<i>Ceratinella scabrosa</i> (O.P.-Cambridge, 1863) (Linyphiidae)	43.48
	<i>Diplocephalus picinus</i> (Blackwall, 1841) (Linyphiidae)	82.86
	<i>Enoplognatha ovata</i> (Clerck, 1757) (Theridiidae)	14.29
	<i>Macrargus rufus</i> (Wider, 1830) (Linyphiidae)	19.05
	<i>Pardosa saltans</i> Töpfer-Hofmann, 2000 (Lycosidae)	66.67
	<i>Tapinocyba insecta</i> (L. Koch, 1869) (Linyphiidae)	56.60
	<i>Tenuiphantes zimmermanni</i> (Betskau, 1890) (Linyphiidae)	85.19
	<i>Monocephalus fuscipes</i> (Blackwall, 1836) (Linyphiidae)	88.92
	<i>Saaristoa abnormis</i> (Blackwall, 1841) (Linyphiidae)	44.44
Woody shrubs (SC) Dominance of Sea Buckthorn (<i>Hippophae rhamnoides</i>) and <i>Calamagrostis epigejos</i> Presence of trees (<i>Crataegus monogyna</i>)		

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Eutrophic wet dune valleys (ES) Humid, Winter inundations High, dense vegetation Dominance of <i>Carex riparia</i>	<i>Centromerita bicolor</i> (Blackwall, 1833) (Linyphiidae)	42.17
	<i>Ceratinella brevipes</i> (Westring, 1851) (Linyphiidae)	29.78
	<i>Clubiona reclusa</i> O.P.-Cambridge, 1863 (Clubionidae)	34.38
	<i>Dicymbium nigrum</i> (Blackwall, 1834) (Linyphiidae)	63.62
	<i>Gnathonarium dentatum</i> (Wider, 1834) (Linyphiidae)	15.63
	<i>Pachygnatha clercki</i> Sundevall, 1823 (Tetragnathidae)	50.86
	<i>Pardosa palustris</i> (Linnaeus, 1758) (Lycosidae)	83.92
	<i>Pardosa pullata</i> (Clerck, 1757) (Lycosidae)	71.79
	<i>Pirata latitans</i> (Blackwall, 1849) (Lycosidae)	85.49
	<i>Pirata piraticus</i> (Clerck, 1757) (Lycosidae)	42.19
	<i>Tiso vagans</i> (Blackwall, 1834) (Linyphiidae)	71.12
	<i>Troxochrus cirrifrons</i> (O.P.-Cambridge, 1871) (Linyphiidae)	30.95
	<i>Troxochrus scabrosa</i> (Westring, 1851) (Linyphiidae)	34.57
	<i>Pardosa monticola</i> (Clerck, 1757) (Lycosidae)	53.43
	<i>Agroeca cuprea</i> Menge, 1873 (Liocranidae)	66.98
Mesotrophic grasslands (SG) Dry or humid (winter inundations) Marram and moss dominated dunes (MG) Sandy, scarce vegetation Mainly mosses and lichens <i>Ammophila arenaria</i> -tussocks	<i>Drassodes cupreus</i> (Blackwall, 1834) (Gnaphosidae)	50.05
	<i>Dysdera crocata</i> C.L. Koch, 1838 (Dysderidae)	17.81
	<i>Metopobactrus prominulus</i> (O.P.-Cambridge, 1872) (Linyphiidae)	37.83
	<i>Poeciloneta variegata</i> (Blackwall, 1841) (Linyphiidae)	15.79
	<i>Sitticus saltator</i> (O.P.-Cambridge, 1868) (Salticidae)	32.50
	<i>Thanatus striatus</i> C.L. Koch, 1845 (Thomisidae)	39.97
	<i>Pardosa proxima</i> (C.L. Koch, 1847) (Lycosidae)	57.14
	<i>Agyneta subtilis</i> (O.P.-Cambridge, 1847) (Linyphiidae)	29.70
Antropogenic disturbed sandy soils (SA) Bare sand, human activities Dense shrubs (DS) Dominance of <i>Hippophae rhamnoides</i> and <i>Ligustrum vulgare</i>	<i>Gongylidium rufipes</i> (Linnaeus, 1758) (Linyphiidae)	61.78
	<i>Microneta varia</i> (Blackwall, 1841) (Linyphiidae)	24.48
	<i>Ozyptila praticola</i> (C.L. Koch, 1837) (Thomisidae)	31.43
	<i>Pholcomma gibbum</i> (Westring, 1851) (Theridiidae)	11.54
	<i>Walckenaeria cucculata</i> (C.L. Koch, 1836) (Linyphiidae)	43.50
	<i>Agyneta decora</i> (O.P.-Cambridge, 1871) (Linyphiidae)	10.77
Degradating Shrub (CS) Shrub with open patches, colonized by <i>Calamagrostis epigejos</i>		

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Humid	<i>Ceratinella brevis</i> (Wider, 1834) (Linyphiidae)	22.00
	<i>Kaestneria pullata</i> (O.P.-Cambridge, 1863) (Linyphiidae)	41.95
Wet rough litter rich vegetation (ESR)	<i>Clubiona phragmites</i> C.L. Koch, 1843 (Clubionidae)	35.71
Rough, eutrophic vegetation	<i>Xysticus ulmi</i> (Hahn, 1831) (Thomisidae)	16.67
Inundations, no management	<i>Agyneta conigera</i> (O.P.-Cambridge, 1863) (Linyphiidae)	11.48
Dry dense grasslands-shrub mosaics (AG)	<i>Hahnia nava</i> (Blackwall, 1841) (Hahniidae)	31.79
Mosaics of low shrubs and <i>Avenula</i> -grassland	<i>Metellina mengei</i> (Blackwall, 1870) (Tetragnathidae)	14.29
Dry, no management	<i>Maso gallicus</i> Simon, 1894 (Linyphiidae)	20.21
	<i>Philodromus cespitum</i> (Walckenaer, 1802)	17.54
High dwarf shrubs (RP)	<i>Alopecosa cuneata</i> (Clerck, 1757) (Lycosidae)	28.18
Dominance of <i>Rosa pimpinellifolia</i> and <i>Arrhenaterium elatius</i>	<i>Heliophanus flavipes</i> (Hahn, 1832) (Salticidae)	26.67
High grass layer	<i>Xysticus erraticus</i> (Blackwall, 1834) (Thomisidae)	36.42
Presence of litter	<i>Trachyzelotes pedestris</i> (C.L. Koch, 1837) (Gnaphosidae)	27.78
Mesotrophic dune valleys (MS)	<i>Arctosa leopardus</i> (Sundevall, 1833) (Lycosidae)	33.79
Dominance of <i>Juncus subnodulosus</i>	<i>Clubiona trivialis</i> C.L. Koch, 1843 (Clubionidae)	36.11
Yearly mowed	<i>Collinsia innerans</i> (O.P.-Cambridge, 1855) (Linyphiidae)	20.00
Winter inundations	<i>Erigone arctica</i> (White, 1852) (Linyphiidae)	65.51
	<i>Erigone promiscua</i> (O.P.-Cambridge, 1873) (Linyphiidae)	74.74
	<i>Prinerigone vagans</i> (Audouin, 1826) (Linyphiidae)	56.45
	<i>Gongylidiellum vivum</i> (O.P.-Cambridge, 1975) (Linyphiidae)	39.46
	<i>Oedothorax apicatus</i> (Blackwall, 1850) (Linyphiidae)	41.59
	<i>Oedothorax fuscus</i> (Blackwall, 1834) (Linyphiidae)	74.22
	<i>Oedothorax retusus</i> (Westring, 1851) (Linyphiidae)	58.23
Short Mesotrophic grasslands (RG)	<i>Thyphochrestus digitatus</i> (O.P.-Cambridge, 1872) (Linyphiidae)	42.21
Wet (inundating) or dry, rabbit grazed	<i>Clubiona frisia</i> Wunderlich & Schuett, 1995 (Clubionidae)	75.41
Marram dunes (MD)	<i>Clubiona subtilis</i> L. Koch 1867 (Clubionidae)	31.07
Dominance of Marram grass (<i>Ammophila arenaria</i>)	<i>Micaria pulicaria</i> (Sundevall, 1831) (Gnaphosidae)	55.56
Strong wind dynamics, close to the sea	<i>Porrhomma microphthalmum</i> (O.P.-Cambridge, 1871) (Linyphiidae)	14.81
Scarce vegetation	<i>Tibellus maritimus</i> (Menge, 1875) (Thomisidae)	18.52
	<i>Trochosa ruricola</i> (De Geer, 1778) (Lycosidae)	28.70

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Moss dominated dunes & Marram dunes near the inner dune front (GD)	<i>Alopecosa fabrilis</i> (Clerck, 1757) (Lycosidae)	20.85
Dominance of lichens and mosses	<i>Micaria dives</i> (Lucas, 1846) (Gnaphosidae)	18.97
Scarce Marram grass vegetation	<i>Walckenaeria stylifrons</i> (O.P.-Cambridge, 1875) (Linyphiidae)	30.38
Near inner dune front	<i>Zelotes longipes</i> (L. Koch, 1866) (Gnaphosidae)	66.70
Dry mesotrophic grasslands (RGD)	<i>Pelecopsis parallella</i> (Wider, 1834) (Linyphiidae)	35.81
Rabbit grazed, short grass layer	<i>Trichopterna cito</i> (O.P.-Cambridge, 1872) (Linyphiidae)	45.98
Dominance of <i>Luzula campestris</i>	<i>Cheiracanthium virescens</i> (Sundevall, 1833) (Clubionidae)	51.43
Inundating mesotrophic grasslands (RGI)	<i>Lepthothrix hardyi</i> (Blackwall, 1850) (Linyphiidae)	26.98
Inundating, short <i>Carex</i> -vegetation	<i>Xerolycosa miniata</i> (C.L. Koch, 1834) (Lycosidae)	64.55
Presence of Creeping willow (<i>Salix repens</i>)		

number of species and the total number of specific (indicator) species as a function of the area of moss dominated dune and short dune grassland patches is illustrated in Fig. 3. The relationship between patch size and total number of species is not significant for either the moss dominated or the short dune grasslands (Fig. 4: Pearson correlation, $r < 0.20$; $P > 0.05$). The number of resident indicator species however is higher in large patches in both vegetation types (Fig. 4: Pearson correlation for moss dunes: $r = 0.87$, $P < 0.01$ and for dry mesotrophic dune grasslands: $r = 0.93$, $P < 0.01$).

DISCUSSION

Our results indicate that almost all dune system habitat types are characterized by the presence of indicator species, dependent on the cluster level. Desender (1996) showed that typical dune carabid species have a strong year-to-year fluctuation in population size, but were never completely lacking from the samples. This variation could be explained by variation in climatological variables. We therefore used only absence/presence data, so true indicators that are always present (independent of their yearly abundance) are unambiguously identified. Besides year-to-year fluctuations, species assemblages can vary as a function of habitat conditions and landscape structure. Our analysis is based on an extensive data set from habitats of different size and

from different landscape configurations, so the determined indicator species can be used as bio-indicators for future monitoring of the management of both open (dominance of grasslands, Marram dunes) and closed (shrub dominated) dune landscapes.

That fact that the variation in species assemblages can be explained by variation in the vegetation structure or succession stage is not surprising and has been documented several times in other studies of invertebrate assemblages (spiders: Duffey 1968; Almquist 1973; carabid beetles: Desender et al. 1992; Empidid and dolichopdid flies: Pollet & Grootaert 1996). Our study indicates the importance of atmospheric and soil humidity as a second important assemblage structuring component since wet vegetation types are clearly separated from dry ones, and Marram dunes near the seaside were separated from those of drier more inland dunes. The importance of atmospheric humidity is demonstrated by the presence of species from dune valleys (*Clubiona frisia* and *C. subtilis*) in Marram dunes near the seaside, while they are completely absent from the same habitat near the inner dune front (1–2 km from the seaside), where atmospheric humidity is significantly lower (Provoost & Hoffmann 1996). The same phenomenon (defined as a double ecological occurrence) has also been documented by Duffey (1968) in British coastal dunes. A third

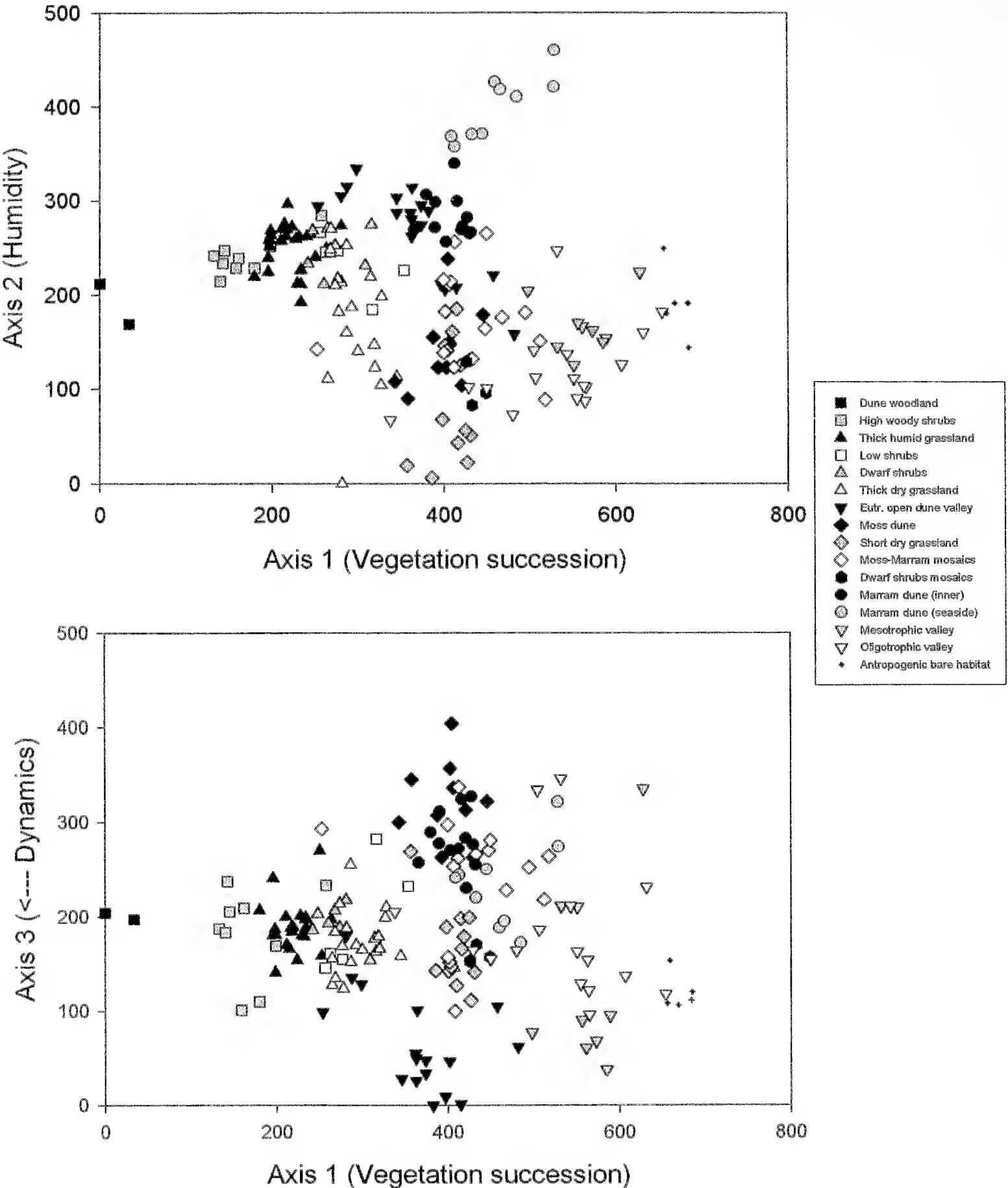


Figure 2.—DCA ordination of the pitfall data based on the species absence/presence data with indication of the habitat type. Above: ordination along the first and second axes; below: ordination along the first and third axes.

important abiotic source of variation is defined here as habitat disturbance. The third axis separates stable habitats without disturbance (woodland, shrubs, dwarf shrubs, rough permanent grasslands) from habitats with high natural (inundations: wet open dune slacks;

eolic dynamics: Marram dunes, bare dunes) or anthropogenic disturbance (grazing and mowing management). These habitats are characterized by ruderal species like *Erigone atra*, *E. dentipalpis*, *E. arctica*, *Oedothorax fuscus*, *O. retusus*, *O. apicatus* and *Bathypantes*

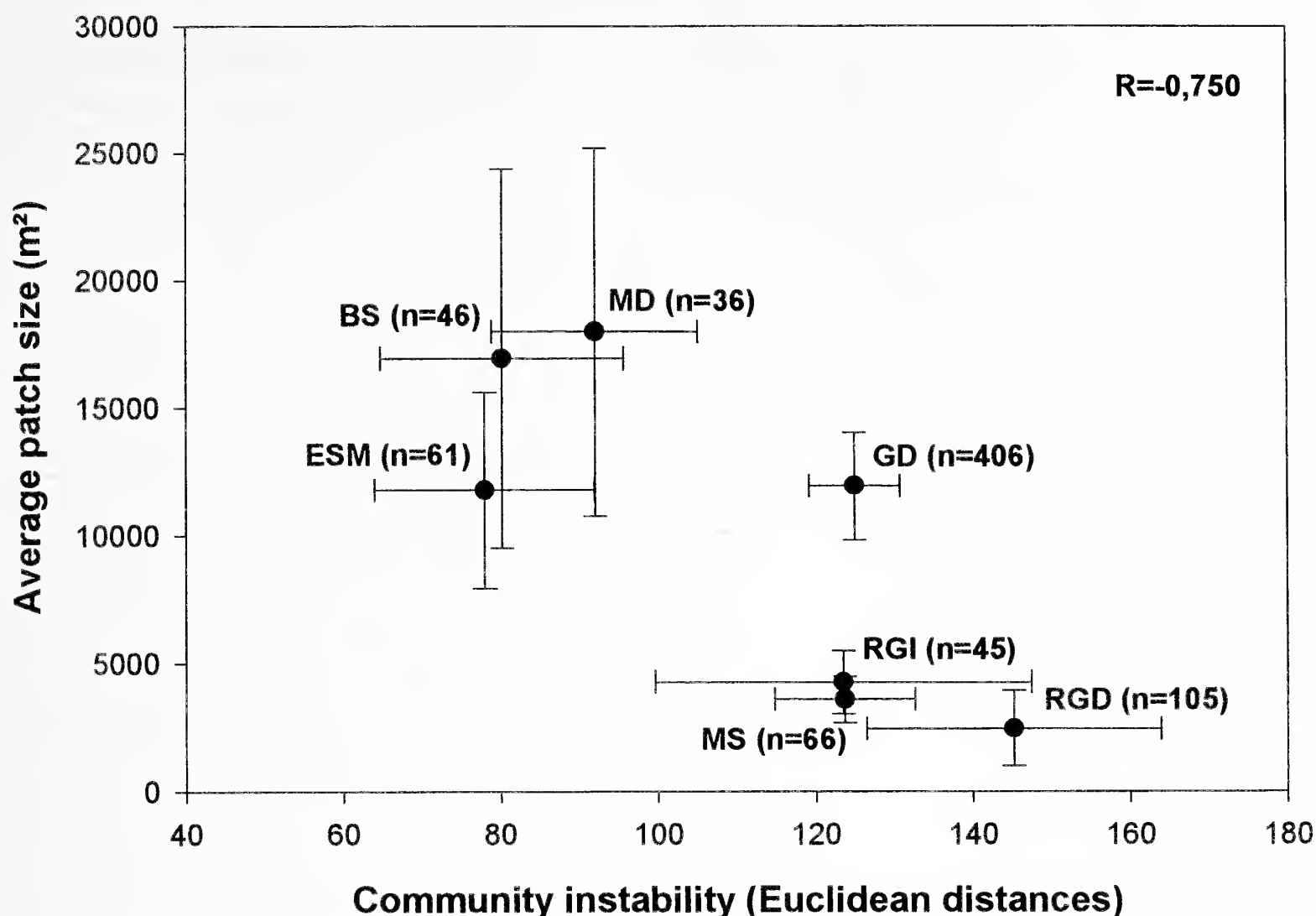


Figure 3.—Assemblage instability of fragmented grassland and dune valley habitats (mean Euclidean distances of DCA scores and 95% confidence intervals; n = number of distance measurements) in function to the average habitat patch size (means and 95% confidence intervals). For abbreviations see Table 2.

gracilis which are all short-living spiders with a rapid juvenile development and a well developed ballooning dispersal capacity.

This data analysis is based only on the presence of adult spiders. Earlier studies have indicated that species typical for open habitats like short grasslands and moss dominated dry dunes (grey dunes) need proximate patches of dense and litter-rich vegetation for their juvenile development and/or retreat during unfavorable periods in their mature life-stage (Bonte et al. 2000 a & b). Thus, habitat variation can strongly alter the presence of spider species bound to these dense vegetation patches for their juvenile development. Although not documented for spider populations, a minimal patch area can determine the presence of viable population size (Hanski 1999). In both cases, an increasing patch area should affect the spider assemblage directly because patch area influences the population size or indirectly because an increasing patch size enhances internal microhabitat variation. Our results on the assemblage level show that the

stability in species composition of spider assemblages in patchy habitats depends on the mean patch area, indicating that differences in the spider assemblage vary more in small habitat patches than in larger ones. Edge effects in small habitats can alter the spider assemblage dramatically, because of the intrusion of species typical for other habitat types in the patch, due to the high circumference-surface ratio. This is certainly true for moss dominated dunes and short grasslands: total species numbers do not differ as a function of the patch size while the number of indicator species significantly increases with an increasing patch size. An explanation of this species-area relationship cannot be given without further research on both internal microhabitat heterogeneity and minimal population sizes. Variation in soil conditions can explain the aggregation of soil-dwelling arthropods like springtails *Collembola* (Bonte & Mertens, unpub. data). Since these are the main prey for typical juvenile wolf spiders and adult dwarf spiders, a larger patch size can alter the total

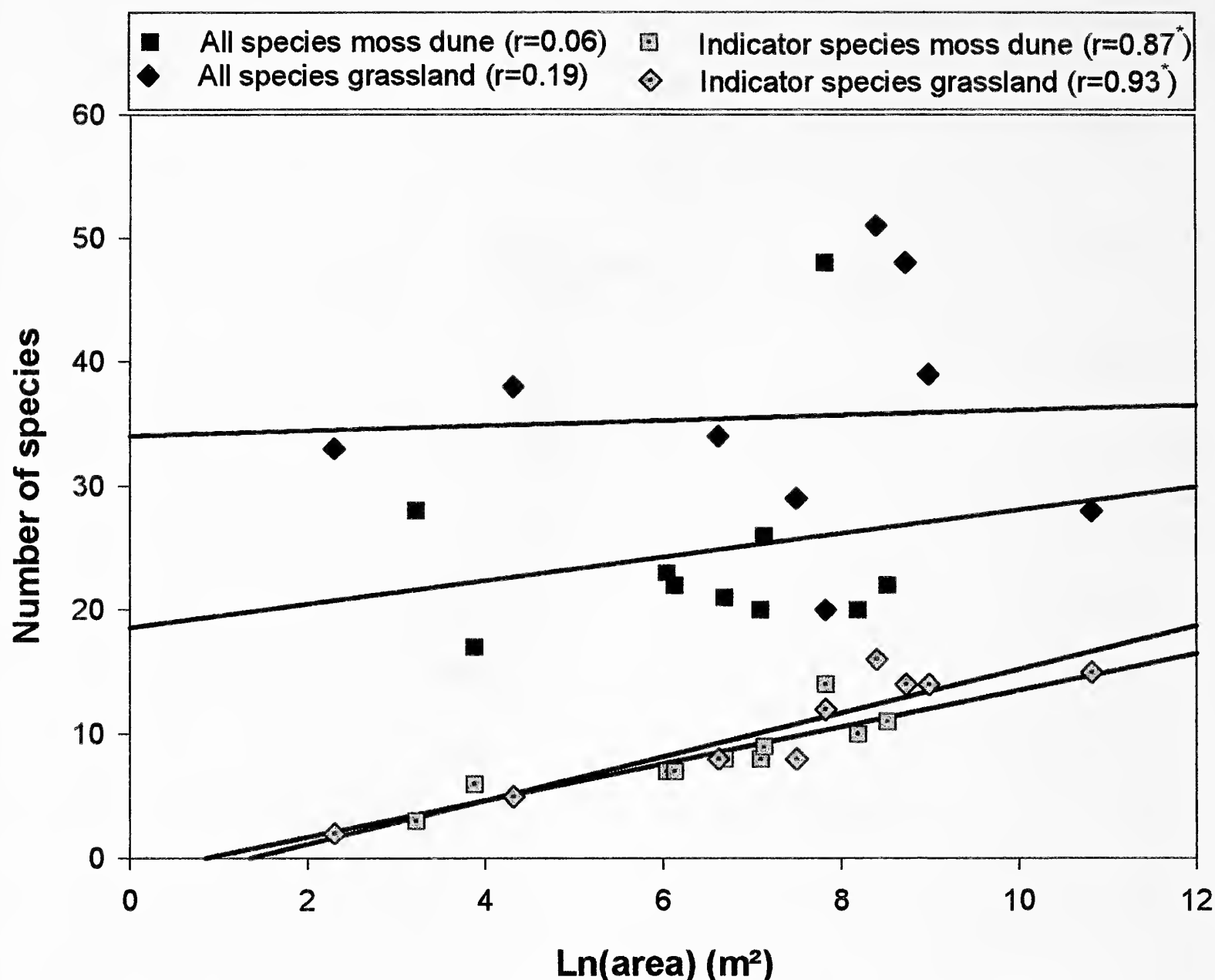


Figure 4.—Species-area relationship for all species and indicator species caught on moss dominated dry dunes and short grasslands from different sizes (Spearman correlation, *: $P < 0.01$).

number of indicator species indirectly by the presence of higher internal microhabitat variation. For the study of minimal patch size and related population size, more detailed studies are needed on meta-population dynamics, based on the survey of a higher number of habitat patches.

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DIVERSITY OF SPIDERS (ARANEAE) IN A SAVANNA RESERVE, NORTHERN PROVINCE, SOUTH AFRICA

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ABSTRACT. In this study our objectives were to describe the diversity and characteristics of spider families occurring in a range of habitat types within a typical savanna ecosystem, to assess the influence of habitat type and seasonality on spider diversity and to determine levels of similarity between habitat types based on species composition. The study was conducted at Makalali Private Game Reserve, Northern Province, South Africa. Five different habitat types were sampled using four trapping techniques (sweeping, beating, active searching and pitfalls). A total of 4832 individuals including 268 species from 38 families were sampled during the study. Families showed varying degrees of habitat fidelity with some being widespread and abundant while others were restricted to a single site and were locally rare. Sites with similar habitat types showed a similarity in spider family composition. All sites have unique species compositions and overall diversity, evenness and richness of spiders do not differ with habitat type. However, analyses of functional groups, e.g., web builders and plant wanderers, showed the positive influence of structural complexity of the habitat. The presence of unique species in all habitats highlights the importance of conserving as wide array of representative habitats within ecosystems. The appearance of strong seasonal patterns in species composition also has important implications for the development of protocols for sampling species diversity. The savanna has a surprising diversity of spiders when compared to other biomes surveyed in South Africa. Factors influencing this diversity beyond the broader habitat variables measured in this study need to be investigated.

Keywords: Diversity, savanna, habitat types, seasonality, sampling techniques

In the past, invertebrates were largely ignored in conservation and only incidentally conserved in existing parks and reserves (De Wet & Schoonbee 1991). People are increasingly aware of threats to biodiversity and there is a growing need to conserve all species, not only the large vertebrates. However, meaningful conservation cannot take place if the species involved are not known (De Wet &

Schoonbee 1991). Surveys of invertebrate fauna in areas where conservation strategies are already in place are especially important. Although not originally established to conserve invertebrates, the resources are already in place for the conservation of potentially new, rare and endemic invertebrate species that could exist in these areas. In addition, management plans to conserve the fauna can only be developed and implemented once inventories, or at least partial inventories are completed.

Although considerable effort has been invested in recording spider diversity in tem-

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perate habitats, only recently have studies on species diversity in tropical ecosystems been undertaken (Dippenaar-Schoeman & Jocqué 1997; Russell-Smith 1999). In South Africa most ecological studies on spiders consist of studies in agroecosystems, (Dippenaar-Schoeman 1979; Van den Berg & Dippenaar-Schoeman 1988) forest and pine plantations (Van den Berg & Dippenaar-Schoeman 1988; Van der Merve et al. 1996). Little is known about the composition of arachnid communities in savanna ecosystems, especially undisturbed conserved areas in Africa (Russell-Smith 1999). In Africa, most previous work on the inventory of savanna arachnids has been undertaken for purposes other than biodiversity assessment (e.g., Russell-Smith 1981; Van der Merwe et al. 1996). In addition, previous studies used a restricted range of sampling techniques that are likely to have provided a biased sample (Dippenaar-Schoeman 1979; Van den Berg & Dippenaar-Schoeman 1988; Dippenaar-Schoeman et al. 1999).

Inventories of faunas are essential before we can consider conservation issues and the sustainable use of our biological diversity. The present study based at Makalali Private Game Reserve, Northern Province, South Africa, has contributed to this wider survey of spider fauna in this country. The aims of this study were to investigate the spider species composition in different habitat types within a savanna ecosystem and to compare sites in terms of their family and species composition. The objectives were to: 1. describe the diversity and characteristics of families found in the different habitat types, 2. to assess the influence of habitat types and seasonality on spider diversity and 3. to produce dendrograms of similarity showing the relationships between sites and habitat types based on species composition.

METHODS

Study area.—The study was carried out at the at Makalali Private Game Reserve (29° 09' S, 30° 42' E), a broad-leafed savanna ecosystem. Makalali is situated close to the western border of Kruger National Park and extends over 10,000 hectares. The Reserve is situated on the Lowveld plains (450 m above sea level) of Northern Province, South Africa. The two dominant vegetation types in the reserve are mixed lowveld bushveld and mopane

bushveld (Acocks 1975; Low & Rebelo 1996).

The Reserve has a sub-tropical climate with a wet summer (average annual rainfall 491.5 mm) and a dry winter. The rainy season starts in October with maximum rainfall between November and February. The daytime temperature in summer months can reach as high as 36 °C. Winter evenings and mornings can be chilly (3 °C) while the days are warm (26 °C).

Spiders were sampled throughout the Reserve in five different habitat types. These were identified subjectively based on apparent differences in vegetation type and soil characteristics. The habitat types sampled were three mixed bushveld types all with different soil (fine, medium and coarse sand), mopane bushveld and rocky outcrops.

Spider sampling.—Sampling was conducted over four periods; the preliminary survey (February 1999), late summer (late February ¥ early March 1999), early summer (October–November 1999) and mid-summer (December 1999). Forty sites were surveyed throughout the reserve. Four sampling techniques (sweeping, beating, active searching and pitfall trapping) were used at all sites.

Sweeping.—A sweep net, 0.6 m in diameter with a 1.2 m long handle was swept through the grass and herb layer. Each sweep covered an arc of approximately 1.5 m through the vegetation on every alternate step (Southwood 1978). A sample consisted of two transects of 20 sweeps each, totaling 40 sweeps from each habitat type. The contents from the sweep nets were placed into a bucket with a small amount of ethyl alcohol to kill all the invertebrates. The contents were sorted on the same day and spiders and other invertebrates were separated from vegetation.

Beating.—Beating was done by firmly striking four branches (all with a diameter of greater than 2 cm) on a tree with a mallet (1.5 kg) ten times each. Eight trees, all different species, were selected randomly in all sites. In some habitat types, e.g. mopane woodland, it was not possible to sample different tree species as the habitat was dominated by a single tree species, *Colophospermum mopane*. In this case eight trees of the same species were sampled. A white beating net was held below the branches during beating. A total of 320 beats was taken from each site. The tree species,

height and diameter of the branch being beaten were recorded. The spiders were then removed from the net with a mouth suction sampler and placed into a sample jar (Sutherland 1996).

Active searching.—In February and March 1999 active searching was conducted on a catch per unit area basis. It was done by marking off two quadrats of 2 m x 2 m (8 m²) in each habitat. Each quadrat was selected at random at least 10 m from any another quadrat. The ground, shrubs, rocks, logs and stones were thoroughly searched for spiders. Each site was searched for a total of 2 hours. In the summer samples (October–November and December 1999) the sampling protocol was changed to include eight quadrats of 1 m x 1 m each. This represented the same area searched (8 m²) as before and the same amount of time (2 hours) was spent searching. It also allowed for an increase in heterogeneity into samples. Spiders were collected using either the hand to jar technique or a mouth suction sampler (Sutherland 1996). Specimens from a single quadrat at each habitat type were pooled for analysis.

Pitfall trapping.—Glass test tubes (25 mm diameter x 150 mm depth) were used as pitfall traps in each habitat. These were inserted into the ground so that the lip was flush with the soil surface and contained a 20 ml solution of 3 parts 70% ethyl alcohol and 1 part 30% glycerol (Samways 1996). The ethyl alcohol acted as a preserving agent and the glycerol prevented the ethyl alcohol from evaporating. They were arranged in two by five grids with traps placed 10 m apart. Traps were left for a period of two weeks and the contents of the pitfall traps were collected and placed into a sample bottle and later spiders were separated from the other invertebrates. Spiders were sorted into morphospecies and the other invertebrates sorted to order level.

Family-level identifications were conducted by the first and third authors while the species-level identification was done by the fourth author. The lack of taxonomic expertise in Africa within certain families, e.g. Lycosidae, makes the identification to species level in some instances impossible. Species level identifications were further hampered in the case of immature specimens and juveniles. In these cases the individuals were only identified to family and where possible to genus.

Diversity indices.—The diversity, richness, and evenness indices of spider communities were calculated using the SPDIVER.BAS program of Ludwig & Reynolds (1988). Species richness (S) examines the number of species occurring in a habitat. Just S alone, while giving insight into diversity in different habitats, can mask trends in dominance and evenness if there is no consideration of abundance. Overall species richness is the most widely adopted diversity measure. However, shifts towards incorporating species abundance has lead to widespread use of Shannon's index (H').

A diversity index incorporates both species richness (the total number of species) and evenness (how equally abundant the species are), in a single value (Magurran 1988). A diversity index allows comparisons to be made between two habitats. One of Hill's (1973) diversity numbers (N1) was selected for this study: $N1 = e^{H'}$, where H' = Shannon's index. This index is more easily interpreted than other diversity indices (Ludwig & Reynolds 1988). Given that values for diversity indices are often difficult to interpret, species richness and evenness are often presented as separate values. In this form they provide important insights into the ecological changes that occur over time or the differences between ecological communities (Bisby 1995).

When all species in a sample are equally abundant an evenness index will be at its maximum, decreasing towards zero as the relative abundance of the species diverge away from evenness. Hill's ratio (E5) is the least ambiguous, is the most easily interpreted and is independent of the number of species in the sample (Ludwig & Reynolds 1988).

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

Where: λ = Simpson's index = $(\sum_{i=1} P_i^2)$ P_i is the proportional abundance in the i th species and H' = Shannon's index.

All statistical analysis was performed using SPSS (Norusis 1994). Data were normally distributed (Kolmogorov-Smirnov test $P > 0.05$) or log transformed where necessary. A two way ANOVA was done to test for significant differences among habitat types and among the sampling period for diversity, evenness and richness.

Estimated species richness.—The estimated species richness was calculated to determine whether or not the environment had been sufficiently sampled. The Chao 1 estimate was calculated (Colwell & Coddington 1994).

$$S_{\text{Chao 1}} = S_{\text{obs}} + F_1^2 / 2F_2$$

Where: S_{obs} = species observed; F_1 = number of singletons; F_2 = number of doubletons. The Estimate S program (Colwell 2000) was used for the calculation and to generate the data for the species accumulation curves.

Spider functional groups.—Functional groups include species that potentially compete for jointly exploited limited resources (Polis & McCormick 1986). Spiders live in a well defined environment with limitations set by both physical conditions and biological factors (Foelix 1996). They can be grouped into specific functional groups based on available information on their habitat preferences and predatory methods (Bultman et al. 1982). Describing the spider diversity in terms of these groups allows for greater insight into how habitat differences may be reflected in life history strategies. For the present study three main functional groups were recognized, namely plant wanderers (PW), ground wanderers (GW) and web builders (WB), with further subdivisions based on microhabitat and general behavior (Dippenaar-Schoeman et al. 1999).

Similarity analysis.—The degree of association or similarity of sites or samples was investigated using standard ecological techniques of ordination and classification (Southwood 1978). Ordination techniques are frequently used to investigate the overall similarity of sites and establish major groupings.

The term “cluster analysis” encompasses a number of different classification algorithms (Faith 1991). It is a useful data reduction technique that can be helpful in identifying patterns and groupings of objects. The analysis begins with each object in a class by itself (StatSoft 1999). The threshold regarding the decision when to declare two or more objects to be members of the same cluster is lowered. As a result more and more objects are linked together and aggregate (amalgamate) into larger and larger clusters of increasingly dissimilar elements. A dendrogram results and the horizontal axis denotes the linkage dis-

tance (Faith 1991; StatSoft 1999). Clusters (branches) resulting from the analysis can be detected and interpreted (StatSoft 1999).

The statistical analysis program STATISTICA (StatSoft 1999) was used to generate dendrograms. The unweighted pair group average linkage and the Euclidean distances were the parameters selected. The analysis was done using 1. families and 2. species present in the different sites.

RESULTS

Total numbers of species and individuals.—A total of 4 832 individuals from 268 species, 147 genera and 38 families was sampled in Makalali Private Game Reserve during the study period. Table 1 is a summary of the species composition. Voucher specimens were preserved in 70% ethanol and deposited in a reference collection lodged with the Natural Science Museum, South Africa (Accession numbers: DMSA-ARA 346–611). A checklist of spiders collected in this study is presented in Whitmore et al. (2001).

Some families were more widely distributed throughout the Reserve while others were restricted to one or a few habitat types. Two families found at all sites were lynx spiders (Oxyopidae) and jumping spiders (Salticidae). Three families were found in 98% of the sites: nursery web spiders (Pisauridae), orb-web spiders (Araneidae) and crab spiders (Thomisidae). Other families found in more than 75% of all sites included comb-footed spiders (Theridiidae), flat-bellied ground spiders (Gnaphosidae), small huntsman spider (Philodromidae), sac spiders (Miturgidae), large huntsmans spiders (Sparassidae) and wolf spiders (Lycosidae).

Families that were only found at a single site included: six-eyed tunnel spiders (Segestriidae); velvet spiders (Eresidae); six-eyed spiders (Sicariidae); dwarf ring-shield spiders (Anapidae); net-casting spiders (Deinopidae); mesh-web spiders (Dictynidae); funnel-web spiders (Agelenidae) and spurred trapdoor spiders (Idiopidae). It must be noted that although these families were found at only one site, the species were not necessarily rare. They may be cryptic or have a patchy distribution and thus may not have been adequately sampled.

Diversity, evenness and richness indices.—There was no overall significant differ-

Table 1.—Total numbers of spider families, genera, species and individuals sampled from Makalali Private Game Reserve. GW = ground wanderers, PW = plant wanderers and WB = web builders. 1 = white sandy bushveld, 2 = general bushveld, 3 = brown sandy bushveld, 4 = rocky outcrops and 5 = mopane woodland). Numbers in parentheses represent the total number of individuals collected.

Functional group	Family	Total		Habitat type				
		Genera	species	1	2	3	4	5
GW	Gnaphosidae	8	14	9 (25)	9 (24)	6 (23)	7 (38)	8 (37)
	Lycosidae	6	16	7 (13)	10 (19)	4 (16)	4 (7)	8 (18)
	Zodariidae	5	9	2 (2)	3 (3)	1 (1)	2 (2)	5 (6)
	Theraphosidae	4	4	1 (2)	2 (7)	3 (11)	2 (7)	2 (4)
	Caponiidae	1	1					1 (1)
	Corinnidae	3	6	2 (2)	2 (2)	3 (4)	1 (1)	2 (5)
	Ctenidae	3	4	1 (3)	1 (2)	2 (2)	2 (3)	1 (1)
	Prodidomidae	3	2	3 (6)	1 (13)		2 (3)	1 (5)
	Liocranidae	2	2	1 (3)	1 (3)	2 (2)	1 (1)	
	Oonopidae	2	2			1 (1)	1 (1)	1 (1)
	Palpimanidae	2	3		1 (1)	1 (2)	3 (4)	2 (3)
	Selenopidae	2	2					
	Agelenidae	1	1		1 (2)			
	Anapidae	1	1				1 (2)	
	Barychelidae	1	1		1 (1)	1 (2)		1 (1)
	Dictynidae	1	1			1 (1)		
	Idiopidae	1	1	1 (3)				
	Scytodidae	1	3		2 (2)	2 (3)	2 (2)	3 (4)
	Sicariidae	1	2				1 (1)	
PW	Salticidae	15	32	16 (152)	18 (140)	20 (284)	23 (189)	18 (66)
	Thomisidae	15	27	17 (84)	18 (94)	16 (111)	23 (68)	22 (54)
	Philodromidae	5	9	7 (38)	4 (40)	7 (31)	5 (18)	6 (38)
	Pisauridae	5	11	5 (35)	9 (50)	8 (85)	7 (102)	6 (35)
	Oxyopidae	3	19	11 (77)	13 (53)	16 (80)	14 (49)	13 (31)
	Sparassidae	3	5	3 (44)	4 (26)	3 (17)	4 (28)	5 (16)
	Miturgidae	2	7	7 (33)	9 (52)	5 (30)	5 (17)	5 (16)
	Clubionidae	1	2	1 (6)	1 (2)	12 (1)	1 (5)	1 (5)
WB	Araneidae	18	31	14 (437)	19 (242)	20 (196)	22 (288)	18 (317)
	Theridiidae	10	28	8 (60)	14 (58)	17 (75)	13 (106)	13 (32)
	Hersiliidae	2	3	1 (1)	1 (1)	3 (17)	2 (3)	
	Linyphiidae	2	6	1 (1)	3 (5)	1 (3)	2 (5)	3 (3)
	Pholcidae	2	3	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)
	Tetragnathidae	2	3	1 (11)	1 (3)	1 (15)	2 (12)	1 (35)
	Uloboridae	2	3	1 (5)	1 (2)	1 (4)	1 (3)	
	Deinopidae	1	1			1 (1)		
	Eresidae	1	2				1 (1)	
	Nesticidae	1	1			1 (4)		
	Segestriidae	1	1					1 (1)
TOTAL	37	147	268	121 (1044)	150 (848)	160 (1034)	155 (967)	148 (736)

ence between the diversity ($F_{4, 39} = 2.236, P = 0.094$), evenness ($F_{4, 39} = 1.689, P = 0.184$) or richness ($F_{4, 39} = 1.766, P = 0.167$) among the different habitat types (Figs. 3a, b & c). When analyzed by sampling period there was a significant difference for the diversity ($F_{2, 39} = 16.779, P < 0.0001$; Fig. 4a) and richness ($F_{2, 39} = 10.253, P = 0.001$; Fig. 4b) but the results were non-significant for evenness ($F_{2, 39} = 2.461, P = 0.106$; Fig. 4c). The diversity and richness follow the same patterns throughout the year, both being highest in midsummer (December). The interaction between the sampling period and habitat type was non-significant for diversity ($F_{8, 39} = 1.157, P = 0.362$), richness ($F_{8, 39} = 1.408, P = 0.242$) and evenness ($F_{8, 39} = 0.848, P = 0.571$). The diversity, evenness and richness

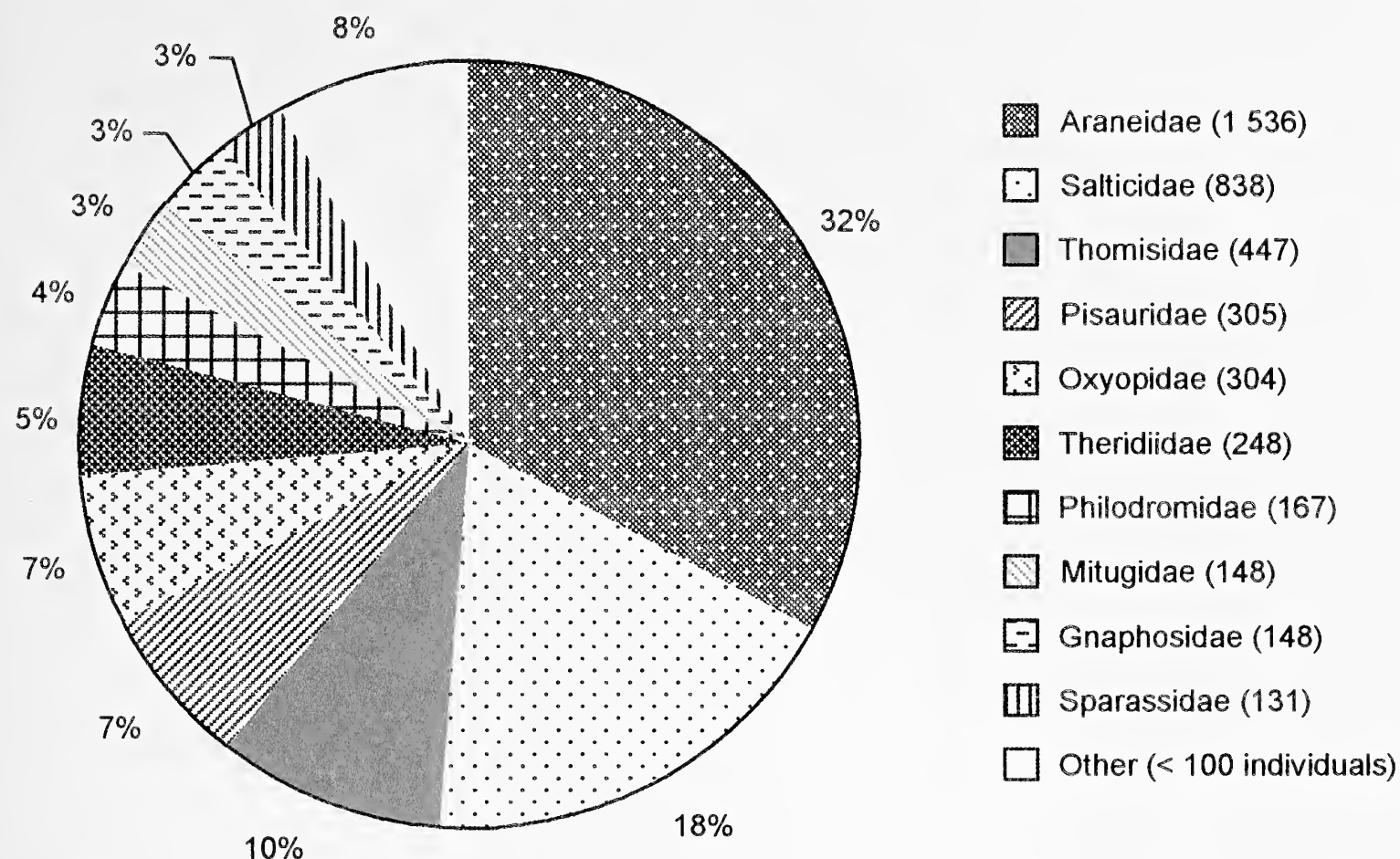


Figure 1.—Family level diversity of spiders at Makalali Private Game Reserve. Percentage abundance of the different spider families (parentheses indicate the number of individuals). The following families have been included in the “other” category Tetragnathidae (75); Lycosidae (71); Theraphosidae (31); Clubionidae (30); Hersiliidae (21); Prodidomidae (19); Uloboridae (17); Linyphiidae (17); Zodariidae (14); Corinnidae (14); Scytodidae (11); Ctenidae (11); Palpimanidae (10); Liocranidae (9); Pholcidae (5); Nesticidae (4); Barychelidae (4); Oonopidae (3); Idiopidae (3); Agelenidae (3); Anapidae (2); Sicariidae (1); Segestriidae (1); Eresidae (1); Dictynidae (1) and Deinopidae (1).

follow the same patterns in the different habitat types at different times of the year i.e. times when diversity is high so was the evenness and richness.

Functional groups and families.—Spiders were divided into three main functional groups: the plant wanderers, ground wanderers and the web-builders. The diversity, richness and evenness values were reassessed at this level to determine if the different life strategies of spiders are influenced in any way by the habitat and or by time as these patterns may be masked by the overall effect of a combined diversity.

Overall, the number of wandering spiders was greater than that of web builders. Plant wanderers were the most abundant and widely distributed. They comprised 48% of all spiders sampled (total individuals = 2239). Web builders comprised 41% (total individuals = 1916) and ground wanderers, 11% (total individuals = 501). The diversity of web-builders was significantly affected by habitat type ($F_{4,39} = 3.452$, $P = 0.022$) but the plant wan-

derers ($F_{4,39} = 0.217$, $P = 0.927$) and ground wanderers ($F_{4,39} = 0.368$, $P = 0.829$) were not (Fig. 5a). The richness was not significantly affected by habitat type for any of the spider functional groups (plant wanderers: ($F_{4,39} = 0.226$, $P = 0.921$), ground wanderers: ($F_{4,39} = 0.898$, $P = 0.480$) and web builders: ($F_{4,39} = 2.243$, $P = 0.093$)) (Fig. 5 b). Similarly the evenness for plant wanderers ($F_{4,39} = 2.735$, $P = 0.051$), ground wanderers ($F_{4,39} = 0.521$, $P = 0.721$) or web builders ($F_{4,39} = 0.491$, $P = 0.743$) was not significantly effected by habitat type (Fig. 5c).

The effect of sampling period on community structure differed slightly from the results for the combined analysis (see previous section). The diversity of plant wanderers was not significantly affected by the sampling period ($F_{2,39} = 1.405$, $P = 0.268$; Fig. 6a) yet the richness ($F_{2,39} = 3.803$, $P = 0.036$) and evenness ($F_{2,39} = 5.482$, $P = 0.011$) were (Figs. 6b & c). The diversity ($F_{2,39} = 15.797$, $P < 0.001$) and richness ($F_{2,39} = 21.102$, $P < 0.001$) of ground wanderers was significantly

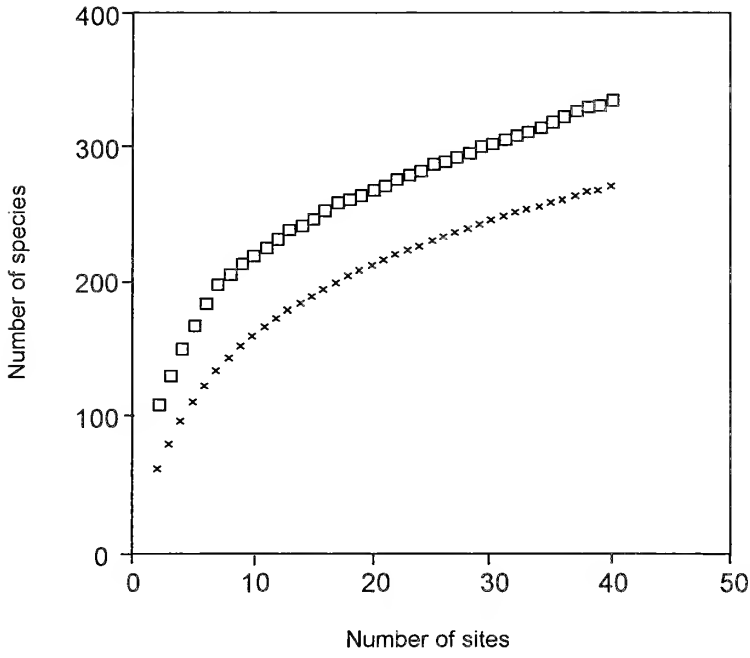


Figure 2.—The observed (□) and estimated (×) species richness for the five different habitat types based on the Chao 1 estimators.

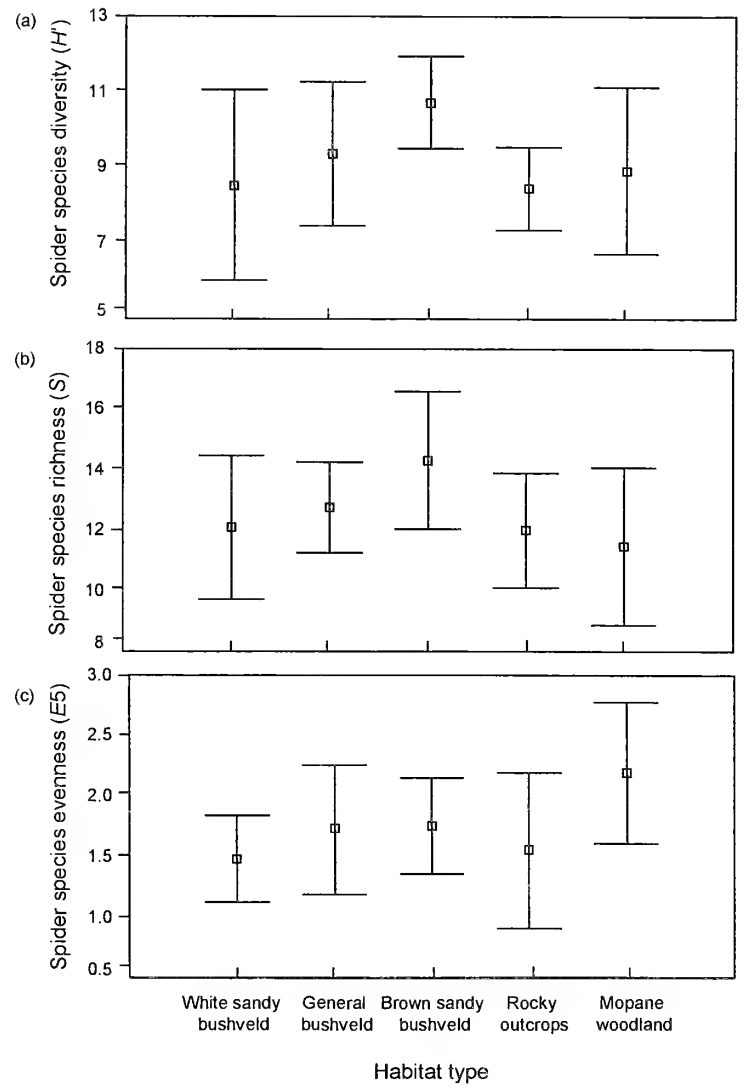


Figure 3.—The influence of habitat type, represented by the mean and \pm 95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. Sample size is eight in each habitat type. There were no statistically significant differences (see text).

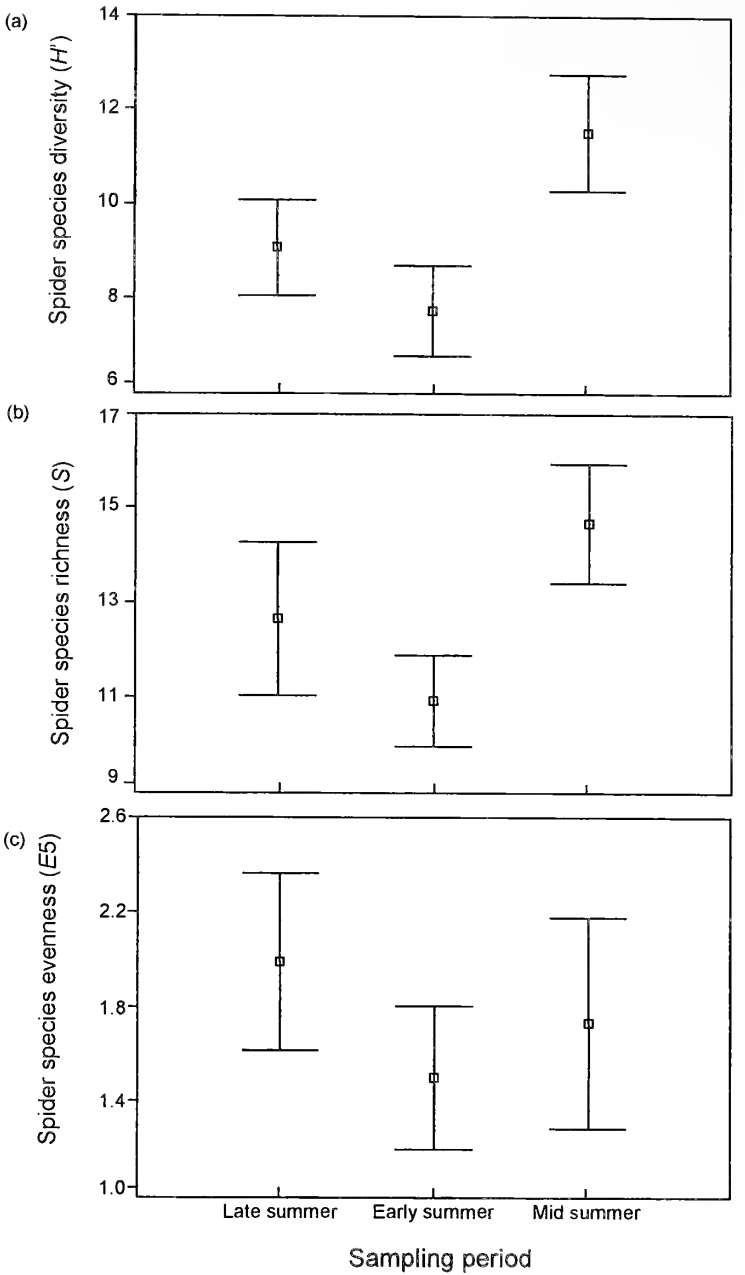


Figure 4.—The influence of sampling period, represented by the mean and \pm 95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. See text for statistical tests.

affected by the sampling period but the evenness ($F_{2,39} = 0.721$, $P = 0.447$) was not (Figs. 6a, b & c). The diversity ($F_{2,39} = 10.013$, $P = 0.001$) and richness ($F_{2,39} = 5.390$, $P = 0.011$) of web builders was significantly affected by the sampling period but the evenness ($F_{2,39} = 1.067$, $P = 0.359$) was not (Figs. 6a, b & c).

Interestingly, there was no overall significance between the evenness and sampling period but when spiders were divided into functional groups, there is an evenness effect with time on plant wanderers. This indicates that at different times of the year different complements of ground wanderer and web building species are dominating the environment and the abundance of these species is relatively uniformly distributed. This means for ground wanderers and web builders we are either

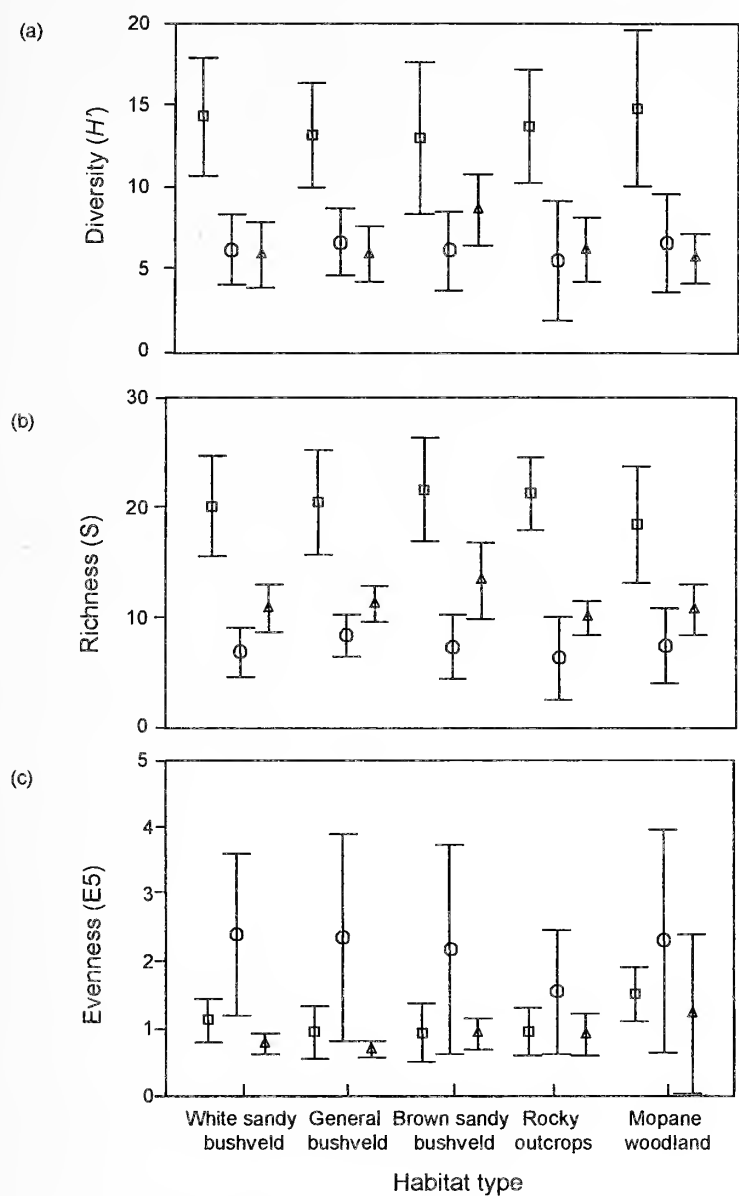


Figure 5.—The effect of habitat type on the a) diversity, b) richness, and c) evenness of spiders at Makalali Private Game Reserve. Spiders have been divided into plant wanderers (□), ground wanderers (○) and web builders (△). The mean and 95% confidence limits are presented. Sample size is eight in all habitat types.

sampling many individuals of the same species or few individuals of many different species at any particular time of the year.

The difference in evenness for plant wanderers with season may be influenced by the structural diversity of the habitat or spider phenology. Therefore, either the plant wanderer evenness is highest when there is maximal structural diversity (mid summer) or at different times of the year there are numerous juveniles of one species and at other times of the year fewer adult individuals of the same species. The only way to get a true habitat type effect on the diversity would be to resample the same sites at the different times of the year.

Similarity analysis.—The family level analysis revealed three main clusters (Figs. 7

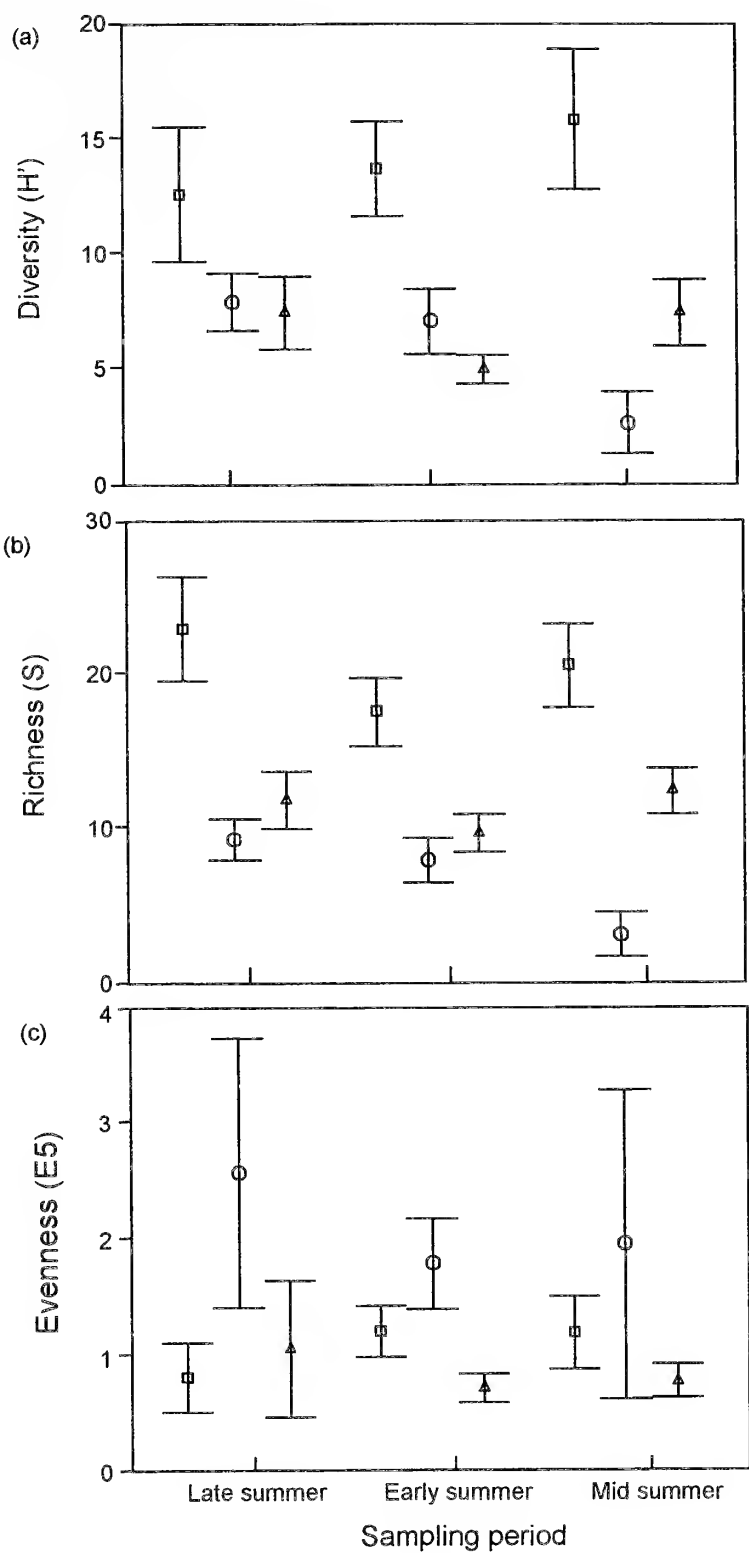


Figure 6.—The effect of sampling period on the a) diversity, b) richness, and c) evenness of spiders at Makalali Private Game Reserve. Spiders have been divided into guilds: plant wanderers (□), ground wanderers (○) and web builders (△). The mean and 95% confidence limits are presented. The sample size is 15 for late and early summer and 10 for mid summer.

& 8a). Cluster A had two sites, 4.6 and 1.3. Cluster B consisted of a combination of habitat types 3, 4 and 5 while cluster C was a combination of mainly habitat types 1 and 2 with two sites from habitat type 3 (Fig. 8a). At the species level there were four distinct clusters (Figs. 7 & 8b). Each cluster had sites from at least four different habitat types (Fig. 8b). At first there did not appear to be any

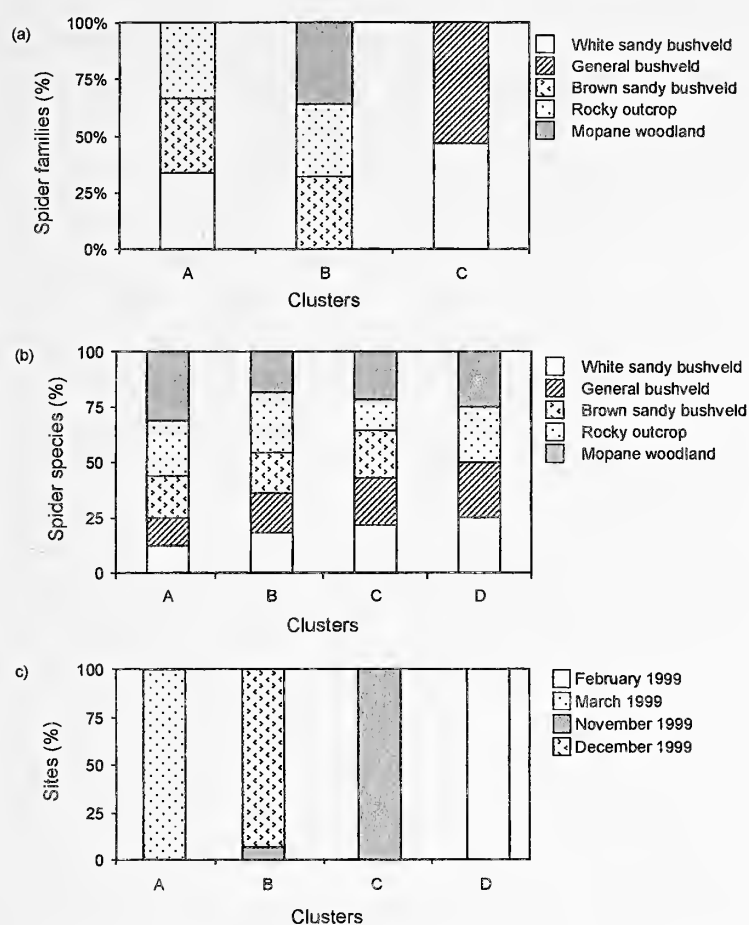


Figure 8.—The percentage of (a) families in clusters A–C, (b) species in clusters A–D and (c) the species clusters A–D according to sampling period. The clusters (A–D) correspond with those of Figure 7.

penaar-Schoeman & Jocqué 1997). The most striking result is the surprisingly high diversity in this savanna biome compared with other biomes that have been surveyed in South Africa. The number of families found here is as high or higher than numbers recorded for other biomes surveyed in South Africa (see Table 3 in Whitmore et al. 2001). Only one study done in the Nama-Karoo (Dippenaar-Schoeman et al. 1999) showed family richness equal to that in our current study. However, that study was conducted over a ten year period and sampling for the present study was done in a single year. The spider family diversity in this savanna biome was therefore surprisingly high (Whitmore et al. 2001). This study illustrates that savanna biomes are very important for the preservation of invertebrate biodiversity and are thus an essential biome to conserve. Furthermore, this study indicates that previous studies of other biomes in South Africa may not be complete. The estimated richness values indicate that even the considerable effort invested in this study failed to sample all the fauna. The families that were abundant were also widely distributed

throughout the Reserve. Some families were not as cosmopolitan and were only found in a single site. Site restriction by some species should not be confused with rarity. Many of these species are cryptic or patchily distributed and were not sampled adequately. Some examples include *Stegodyphus dumicola* Pocock 1898 and the baboon spiders (e.g., *Ceratomyrus bechuanicus* Purcell 1902 and *Pterinochilus nigrofulvus* (Pocock 1898)). *Stegodyphus dumicola* was only sampled in one habitat type but the distribution is known to be extremely patchy (Siebt & Wickler 1988). Numerous nests were observed outside of the immediate sampling areas. This particular group may not have been sampled adequately because of its patchy distribution and not because the species is rare. The theraphosids (baboon spiders) were sampled from all five different habitat types but in low abundances (only 15 individuals were found throughout the Reserve). Low trap catches may be a reflection on an inadequate sampling protocol for this particular taxon. Theraphosids are nocturnal and in this study night sampling was not done. However, additional hand collecting was done and three different theraphosid species were collected from their burrows. These additional species were not found while sampling in the sites. Many theraphosid burrows were observed, especially in the western section of the Reserve in the white sandy and brown sandy mixed bushveld habitats (habitat types 1 and 2).

Diversity, evenness and richness.—There are many environmental factors that affect species diversity. Some of these factors include: 1. seasonality, 2. spatial heterogeneity, 3. competition, 4. predation, 5. habitat type, 6. environmental stability and 7. productivity (Rosenzweig 1995). If spider family distribution was affected by a single factor, e.g. the habitat type, we would expect all sites within a habitat type to have high similarity values and share little with other sites.

Diversity values varied considerably between the different sites and similar habitat types did not necessarily have similar diversities. There was no overall significant difference between the diversity, evenness or richness among the different habitat types. This is surprising because we would expect bushveld habitat types (types 1–4), a combination of different trees, herbs and shrubs (structurally

complex), to have a higher diversity than the mopane woodland habitat type as this habitat type is dominated by a single tree species (*Colophospermum mopane*). However, this was not the case and although the mopane woodland appears to be a more barren habitat (floristically) it still has a high spider diversity.

The results indicate that all sites have unique species compositions. Additionally, there are many factors that determine the species composition at a site and not simply the habitat type. An alternative interpretation of this is that the habitat types classified as different at the start of the study may be more similar than previously thought.

However, when spiders were divided according to their functional group there was a significant effect of habitat on the diversity of web builders and the evenness of plant wanderers. The web building and plant wandering spiders rely on vegetation for some part of their lives, either for finding food, building retreats or for web building. The structure of the vegetation is therefore expected to influence the diversity of spiders found in the habitat. There were many more plant wanderers and web builders sampled than ground-dwellers. This again indicates that structural diversity of the vegetation may, in some way, influence the spider diversity.

Studies have demonstrated that a correlation exists between the structural complexity of habitats and species diversity (Uetz 1979; MacArthur 1964; Pickett et al. 1991; Andow 1991; Hawksworth & Kalin-Aroyo 1995; Rosenzweig 1995). Diversity generally increases when a greater variety of habitat types are present (MacArthur 1964; Ried & Miller 1989; Cook 1991; Hawksworth & Kalin-Aroyo 1995).

Uetz (1991) suggests that structurally more complex shrubs can support a more diverse spider community. Downie et al. (1999) and New (1999) have demonstrated that spiders are extremely sensitive to small changes in the habitat structure, including habitat complexity, litter depth and microclimate characteristics. Generally, as disturbance increases the spider species richness decreases. Thus the physical structure of environments has an important influence on the habitat preferences of spider species, especially web-building species (Uetz 1991; Hurd & Fagon 1992).

All habitat types have unique families and species indicating that all habitats are important if the spider biodiversity is to be conserved. Therefore, no one habitat type is less important than another and efforts should be made to conserve representatives of all habitat types within the Reserve. Habitat type seems to influence the spider composition at the family level because similar families cluster within a similar habitat type. However, for species, the habitat type does not seem to affect the community composition. According to the cluster analysis, the results at the level of species closely corresponded to the sampling periods. This indicates that similar species are present at specific times of the year. Thus, at the scale measured, seasonal variation may be a more important determinant than the habitat type alone. This provides valuable insight into sample protocols and certain species may dominate at different times of the year. Therefore, to get a true representation of the species present sampling should be conducted in all seasons. This conclusion is supported by other work being conducted in the Reserve on other invertebrates (beetles, ants and grasshoppers) where different species dominated at different times of the year. In addition, certain species may mature at different times of the year and thus by conducting sampling throughout the year adults can be collected. The adults are taxonomically important, as they are often essential for species level determinations.

The savanna habitat has a surprisingly diverse spider community and further research should be encouraged in this biome. However, to maintain and manage this high diversity factors other than habitat type need to be identified. Factors at the microhabitat scale, which may be important in influencing the diversity, need to be investigated.

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THE NEGLECTED COUSINS: WHAT DO WE KNOW ABOUT THE SMALLER ARACHNID ORDERS?

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ABSTRACT. An overview of the systematics of smaller arachnid orders (Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae and Pseudoscorpiones) is provided, along with data on numbers of recognized families, genera and species for each group. The micro-diverse orders, Opilioacariformes (1 family, 9 genera, 19 species), Ricinulei (1 family, 3 genera, 55 species), Palpigradi (2 families, 6 genera, 78 species), Uropygi (1 family, 16 genera, 103 species), Amblypygi (5 families, 17 genera, 136 species) and Schizomida (2 families, 34 genera, 205 species), are amongst the smallest of all terrestrial arthropod orders. The meso-diverse orders, Solifugae (12 families, 140 genera, 1,087 species) and Pseudoscorpiones (24 families, 425 genera, 3,239 species)—along with the Scorpiones (1,279 species) and Opiliones (c. 6,000 species) which are not dealt with in this contribution—are dwarfed by the three mega-diverse arachnid orders, Araneae (c. 36,000 species), Parasitiformes and Acariformes (with a combined total of c. 48,000).

Keywords: Arachnida, Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae, Pseudoscorpiones, diversity, systematics

The Arachnida are a conspicuous and dominant animal group. They have diversified into virtually every terrestrial environment, with a few freshwater and marine representatives. Most are predators, but some are phytophages and others are obligate parasites of animals or plants. Adults range in size from 250 μ m mites to the plate-sized tarantulas. Arachnids include some of the most poisonous animals on Earth—some spiders and scorpions are capable of quickly killing an adult human—and many evoke fear and loathing in human cultures. Some mites and ticks are vectors for debilitating diseases, which cause immeasurable suffering to many humans. Most, however, are harmless to humans and are rarely seen by non-biologists.

Arachnida are traditionally ranked as an arthropod class within the subphylum Chelicerata, alongside pycnogonids, xiphosurans, eurypterids and some other minor extinct taxa. The number of orders recognized within the Arachnida has changed over time and between researchers. The current consensus of 10 non-acarine orders seems to be holding firm, but the number of recognized acarine orders varies from one to nine. For the purposes of this study, I follow Halliday (1998) who treat-

ed three orders, Opilioacariformes, Parasitiformes and Acariformes. Thus, a total of 13 orders are recognized here. While the taxonomic rank assigned to particular monophyletic groups of organisms is immaterial to most systematists (in sharp contrast to the consternation shown by some other sections of the biological community) the relationships between these taxa are of much more interest. Indeed, arachnids have been the subject of several recent phylogenetic treatments, including morphological and molecular data-sets (Kraus 1976; Shultz 1989, 1990; Weygoldt 1998a; Weygoldt & Paulus 1979a, 1979b; Wheeler & Hayashi 1998). Results obtained from these studies are not, however, uniform, and considerable differences exist in hypothesized relationships between orders (Figs. 1, 2).

Arachnids have a long ancestry. At least three Recent orders appeared in the fossil record during the Silurian or Devonian, and most of the remaining extant orders appeared by the Carboniferous (Selden 1993). Scorpions possess the longest lineage and have been found in Upper Silurian marine sediments. Morphological evidence suggests that Silurian scorpions were all aquatic. Trigonotarbid also

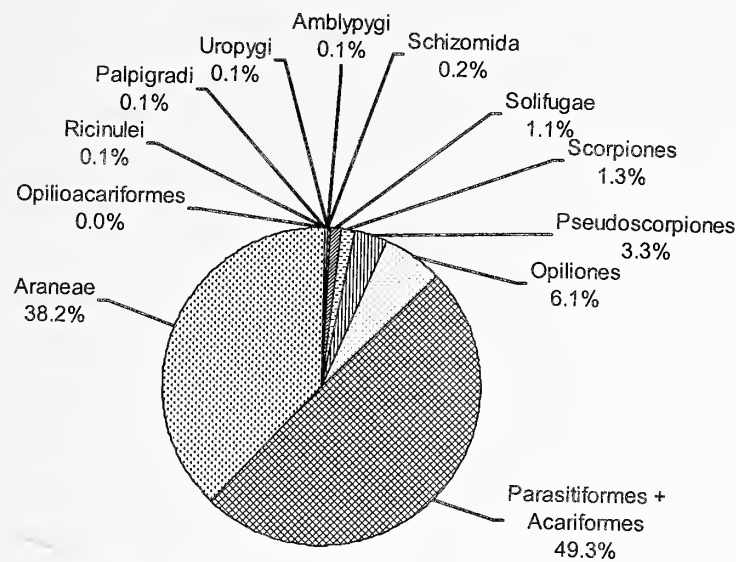


Figure 3.—Chart depicting proportion of described, valid arachnid species showing the numerical dominance of the Araneae and the two major orders of Acari, Parasitiformes and Acariformes.

entire number of species in one of the other arachnid orders. Spiders now total 37,296 described species (Platnick 2001), and the Acari (Opilioacariformes + Parasitiformes + Acariformes) are estimated to include some 48,200 described species (Halliday et al. 2000). This rich diversity is accompanied by varied morphological and ecological traits.

The four meso-diverse orders—Opiliones, Pseudoscorpiones, Scorpiones and Solifugae—possess more than 1,000 named species, but do not, and will not, approach the levels of diversity seen in the Araneae or Acari. The Opiliones are the most diverse with an estimated 6,000 described species (J.C. Cokendolpher, pers. comm.). Pseudoscorpiones con-

tain 3,239 described species, with the Scorpiones (Fet et al. 2000) and Solifugae possessing 1,279 and 1,087 described species, respectively.

The micro-diverse orders—Schizomida, Amblypygi, Uropygi, Palpigradi, Ricinulei and Opilioacariformes—include some of the most geographically restricted arthropod orders, with none currently possessing more than 210 described species.

The total level of arachnid diversity is hard to assess, as there are still considerable taxonomic impediments to be overcome, mostly in the form of vast numbers of undescribed taxa awaiting description. The current figure of approximately 97,000 described species (Table 1) is likely to represent a small proportion of the total diversity. Continued funding for taxonomic research, particularly in tropical and southern temperate regions, is of paramount importance if we are to attempt to reasonably assess the total global diversity of these fascinating creatures. Many are undoubtedly being lost through extinction as habitat destruction and modification continues to play a significant role in shaping the destiny of many arachnids.

In this paper I have restricted my discussion to those taxa for which I have compiled sufficient data and for which I have sufficient knowledge to make some observations which may prove to be of interest to readers. I have chosen to concentrate on the “smaller” orders as they are often neglected in deference to the

Table 1. Arachnid orders with numbers of valid Recent described taxa to December 2000. Figures in italics are estimates only.

Order	Families	Genera	Species	Authority
Opilioacariformes	1	9	20	this paper
Ricinulei	1	3	55	this paper
Palpigradi	2	6	78	this paper
Uropygi	1	16	106	this paper
Amblypygi	5	17	136	this paper
Schizomida	2	34	205	this paper
Solifugae	12	141	1,087	this paper
Scorpiones	16	155	1,279	Fet et al. (2000)
Pseudoscorpiones	24	425	3,239	Harvey (1991); this paper
Opiliones	25	500	6,000	J.C. Cokendolpher, pers. comm.
Araneae	106	3,450	37,296	Platnick (2001)
Parasitiformes + Acariformes	350–422	3,300–4,000	48,181	Adis & Harvey (2000), Halliday et al. (2000)
TOTAL	545–617	8,055–8,755	97,682	

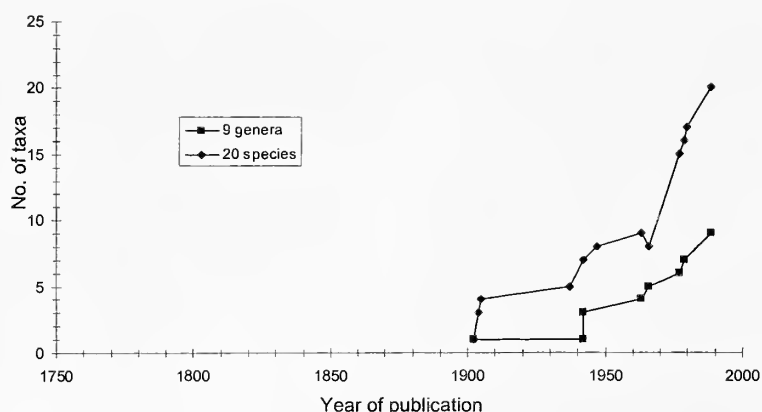


Figure 4.—Numbers of valid Recent opilioacariform genera and species.

three dominant arachnid orders mentioned above. Similar data on two other meso-diverse orders, Scorpiones and Opiliones, have not been compiled.

Despite their modest levels of diversity, there have been several recent breakthroughs in our understanding of the relationships within some of these smaller orders that may prove of interest to a wider audience. I treat the orders in sequence from least to most species-rich.

METHODS

The graphs presented below (Figs. 4–7, 9, 11, 12, 14) were produced from a primary database that I maintain as part of my systematic research and cataloguing activities. This database is current to December 2000. The date of description of a new taxon, in this case genus or species, was transferred to an Excel 2000 spreadsheet to produce the cumulative plots. I also included taxa that are currently treated as junior synonyms, but deleted one taxonomic unit when the taxon's name was judged to have been first placed in synonymy. This provided an estimate of the number of taxa recognized at any one time, although species which were treated as synonyms for part of their "life" but are currently recognized as valid have been treated as having never been synonymized. Homonyms were treated from the year they were first described and not by the date in which they were first given a replacement name.

OPILIOACARIFORMES

The smallest arachnid order, the Opilioacariformes—sometimes termed the Notostigmata or Opilioacarida—was first discovered by With (1902) who briefly described *Opilioacarus segmentatus* With 1902 from Alge-

ria. That was quickly followed by a fully illustrated description of *O. segmentatus* (which was erroneously placed in the new genus *Eucarus*) and the description of *Eucarus italicus* With 1904 from Sicily and *E. arabicus* With 1904 from Aden (With 1904). Since then, 17 additional species have been described, one of which was placed in the synonymy of another. Of these descriptions, most notable were those of Hammen (1966, 1968, 1969, 1971, 1977) and Coineau & Hammen (1979) who had commenced a series of papers on the morphology and taxonomy of the group in which a new generic classification and a phylogenetic analysis was proposed.

The Opilioacariformes consists of a single family, Opilioacaridae, and the 20 named species are currently placed in nine genera (Fig. 4), the majority of which have been described during the past 30 years. They possess uniform morphology but two genera, *Paracarus* Chamberlin & Mulaik 1942 from Kirghizia and *Siamacarus* Leclerc 1989 from Thailand, possess three pairs of lateral eyes (Hammen 1968; Leclerc 1989). The remaining taxa possess only two pairs. Harvey (1996) presented a cladogram of opilioacarid genera, based upon an unpublished cladistic analysis, which suggested that *Paracarus* and *Siamacarus* were the sister-group to the remaining genera. Important publications about opilioacariforms include Chamberlin & Mulaik (1942), Grandjean (1936), Hammen (1966, 1968, 1969, 1971, 1977), Leclerc (1989), Juvara-Bals & Baltac (1977) and With (1904).

RICINULEI

Ricinuleids have often been described as "living fossils" (Selden 1986)—a fitting appellation given their bizarre appearance and gait—but in many respects they are highly modified arachnids with a number of autapomorphies, including a peculiar pre-carapaceal structure, the cucullus, a characteristic mode of sperm transfer and modified pedipalps.

The first Recent ricinuleid species, *Cryptostemma westermanni* Guérin-Méneville 1838 from west Africa, was described by Guérin-Méneville (1838) who attributed the animal to the order Opiliones. A second genus and species, *Cryptocellus foedus* Westwood 1874 was described from Amazonia. Further species have since been described from tropical Africa and America. Ironically, the first

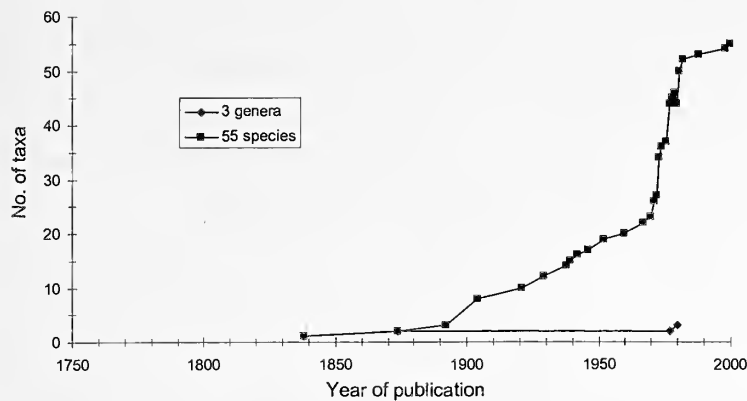


Figure 5.—Numbers of valid Recent ricinuleid genera and species. Note the rapid increase of new species since 1970.

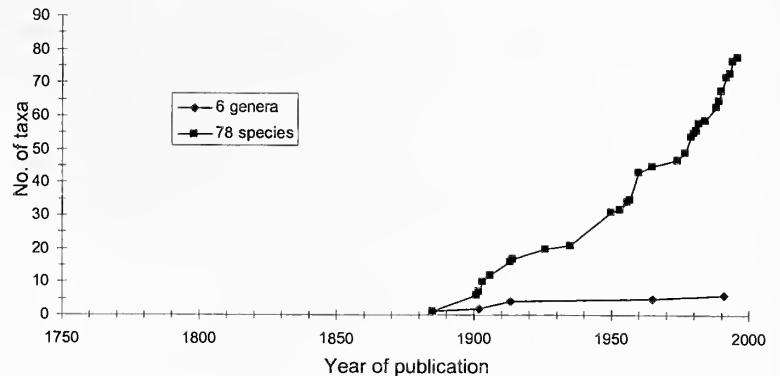


Figure 6.—Numbers of valid Recent palpigrade genera and species. Note the steady increase in described species in the latter part of the 20th century.

species nowadays attributed to the order, *Curculioides ansticii* Buckland (along with *C. prestvicii* Buckland, which is now regarded as a member of the extinct tetrapulmonate order Trigonotarbida), was described in 1837, a year prior to the discovery of living forms. As the name attests, Buckland (1837) erroneously considered that the fossils, from the fossil-rich Carboniferous British Coal Measures, were insects and it was many years before it was discovered that they were in fact arachnids.

Selden (1992) divided the Ricinulei into two suborders: the Neoricinulei for the Recent species of Ricinoididae, and the Palaeoricinulei for the 15 Carboniferous species placed in the Curculioididae and Poliocheridae. The Recent taxa are currently assigned to three genera: *Ricinoides* Ewing 1929 from west and central Africa, and *Cryptocellus* Westwood 1874 and *Pseudocellus* Platnick 1980 from the Americas.

Relationships among the three Recent genera are uncertain, as there are no unambiguous characters which serve to place one genus closer to another. Of the 55 species currently recognized, 37 have been described since 1960 (Fig. 5), and although some are found only in caves, the vast majority are from rainforest habitats. Many species are only known from a single locality, and some may possess naturally small distributions. This places them at risk of extinction through clearing of primary rainforest and similar habitats, especially in West Africa.

Although ricinuleids possess a suite of peculiar features, the most extraordinary is their mode of sperm transfer, which is facilitated by an elaborate copulatory apparatus on the third leg of the male. This structure rivals the morphological complexity of the modified pedi-

palpal tarsus of male spiders which is used for the same purpose. Like the spider pedipalp, the ricinuleid third leg offers numerous species-specific features that are very important taxonomically.

The literature on ricinuleids is not extensive, but important papers include Hansen & Sørensen (1904), Mitchell (1970), Pittard & Mitchell (1972), Tuxen (1974), Platnick & Paz (1979), Platnick (1980), Platnick & Shadab (1981), Legg (1976) and Selden (1992). The Ricinulei are usually placed as the sister-group to the Acari (Shultz 1990; Weygoldt & Paulus 1979b), but Dunlop (1996b) suggested that they represent the sister-group of the Trigonotarbida within the Tetrapulmonata.

PALPIGRADI

Palpigrades are probably the most enigmatic of all of the arachnid orders. They are extremely small and fragile creatures, with a long multi-segmented flagellum that is frequently broken off during collection or from handling preserved specimens. Their relationships are obfuscated by a suite of reductional apomorphies, but they have been either placed within the Tetrapulmonata (e.g. Shultz 1990; Weygoldt & Paulus 1979b) or as a sister-group to the mite order Actinotrichida (Hammen 1982).

The first palpigrade, *Koenenia mirabilis* Grassi & Calandruccio 1885, was described from specimens collected in Sicily, and ascribed to the "Microteliphonida", a name that was promptly changed to Palpigradi by Thorell (1888). The majority of the 78 Recent species have been described since 1950 (Fig. 6) by P. Rémy and B. Condé (see Condé 1996). The order is divided into two families, Eukoeneniidae and Prokoeneniidae. The Euko-

eneniidae comprises four genera with the vast majority of species placed in *Eukoenenia* Börner 1901. The Prokoeneniidae consists of seven species in two genera. The differences between palpigrade genera were summarized by Condé (1996), but there has been no explicit examination of their relationships.

The two fossil species attributed to the Palpigradi add little to our understanding of the group. *Paleokoenenia* Rowland & Sissom 1980, with the sole species *P. mordax* Rowland & Sissom 1980, is from onyx marble in Arizona, suspected to be from the Pliocene (Rowland & Sissom 1980), and is currently not assigned to any family. *Sternarthron* Haase 1890, with *S. zitteli* Haase 1890, is from the Jurassic of Germany, and with a total length of 15 mm (Haase 1890), is substantially larger than any other palpigrade. However, it is probably misplaced within the Palpigradi and may not even be an arachnid (Selden 1993).

The most important contributions to the taxonomy and classification of the order have been made by B. Condé, which were summarized in Condé (1996). Other important references include Hansen & Sörensen (1897), Hansen (1901) and Rowland & Sissom (1980).

UROPYGI

Whip-scorpions are imposing, robust tropical predators with enlarged raptorial pedipalps and a multi-segmented elongate post-pygidium. Like schizomids, they possess anal glands that they use to accurately spray a chemical cocktail to deter predators (Eisner et al. 1961).

Linnaeus (1758) was the first to describe a whip-scorpion, based upon a specimen from "India"—by which he probably referred to the entire east Indies—which he named *Phalangium caudatum* Linnaeus 1758. Linnaeus's use of the generic name *Phalangium* Linnaeus 1758 was quite different to that employed by later biologists, as he included several different arachnids nowadays placed in separate orders. The distinguished invertebratologist P.A. Latreille (1802) was amongst the first to dismember *Phalangium*, and his name *Thelyphonus* Latreille 1802 was the first to be applied solely to a whip-scorpion. Uropygid species were slowly added to the group by 19th century workers, including A.G. Butler, T.

Thorell, R.I. Pocock and K. Kraepelin. F.H. Gravely seems to have been the first uropygid taxonomist with first-hand knowledge of live whip-scorpions which he studied while based at the Indian Museum in Calcutta.

Rowland & Cooke (1973) provided a useful synopsis of the order, including a key to genera and a checklist of species. They also presented a novel classification that included the division of the group into two families, Thelyphonidae and Hypoconidae. Weygoldt (1979) suggested that the existence of two families was not supported by the available data, and Haupt & Song (1996) formally reduced the Hypoconidae to a subfamily as there was little support for a monophyletic Hypoconidae. Dunlop & Horrocks (1996) suggested that the "hypoconids" may be the sister-group to the Schizomida + *Proschizomus* Dunlop & Horrocks 1996, but the character polarities they utilized were regarded as uncertain and many features of *Proschizomus* were not observable in the fossilized material.

Several uropygid genera appear to be unsupported by any apomorphic character states and are clearly paraphyletic. The most glaring example is *Thelyphonus* which is characterized by a series of plesiomorphies. Further research into this, the oldest uropygid genus, would be most welcome to clearly understand the evolutionary relationships of these fascinating animals.

Some 103 whip-scorpion species are currently recognized and placed in 16 genera. Two genera, *Thelyphonus* and *Hypoconus* Thorell 1888, account for nearly half of the species diversity of the order, with some 31 and 19 species, respectively. Nearly two-thirds of the species currently recognized were collected and described over 100 years ago, and the past century has produced only about 40 new species (Fig. 7). Significantly, six of the 16 recognized genera were described in this same interval—all of which contain only one or two species. The validity of many of these taxa has not been rigorously tested, and I suspect that some will eventually prove to be synonyms of older genera once the relationships of whip-scorpions are fully investigated.

The uropygid genera have some level of geographical discreteness, with three major areas of occupancy: the Americas, West Africa and Australasia. The American fauna con-

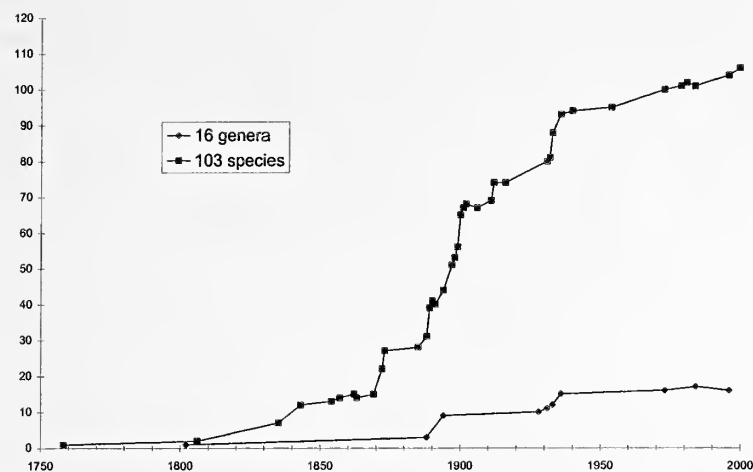


Figure 7.—Numbers of valid Recent uropygid genera and species. Note the rapid increase in described species during the latter part of the 19th century.

sists of three genera and 17 species, *Mastigoproctus* Pocock 1894 (14 species, southern U.S.A. to Brazil), *Thelyphonellus* Pocock 1894 (two species, Brazil, Surinam and Guyana) and *Amauromastigon* Mello-Leitão 1931 (one species, Brazil). The sole West African species, *Etiennius africanus* (Hentschel 1984), is found in Gambia and Senegal. The Australasian fauna, by far the most diverse, ranges from India to Fiji, and comprises 85 species in 13 genera (*Abaliella* Strand 1928, *Chajnus* Speijer 1936, *Ginosigma* Speijer 1936, *Glyptogluteus* Rowland 1973, *Hypoctonus*, *Labochirus* Pocock 1894, *Mastigoproctus*, *Mimoscorpius* Pocock 1894, *Minbosius* Speijer 1933, *Tetrabalius* Thorell 1888, *Thelyphonus*, *Typopeltis* Pocock 1894 and *Uroproctus* Pocock 1894).

Fossil uropygids have been described from Europe and North America, in the Carboniferous genera *Geralinura* Scudder 1884 and *Proschizomus*, the Cretaceous *Mesoproctus* Dunlop 1998 and a species of *Thelyphonus* from the Miocene.

Important papers on the taxonomy of the Uropygi include Kraepelin (1897), Gravely (1916), Millot (1949), Rowland & Cooke (1973) and Dunlop & Horrocks (1996). Although the Uropygi are firmly placed as the sister-group of the Schizomida (which are sometimes included as a suborder of the Uropygi), the systematic position of Uropygi + Schizomida varies. They were treated as the sister-group to the Amblypygi + Araneae by Weygoldt & Paulus (1979b), and as the sister-group to Amblypygi by Shultz (1990), with the entire Pedipalpi (Amblypygi + Schizom-

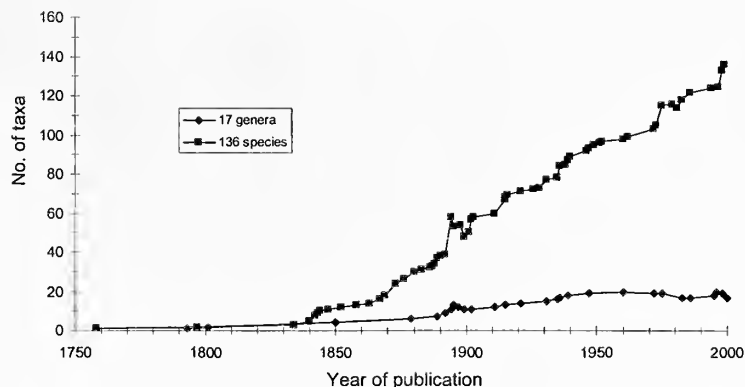


Figure 8.—Numbers of valid Recent amblypygid genera and species. Note the steady increase in new species since the 1880's and the differences in taxonomic opinion between rival taxonomists in the 1890's, when numerous species were synonymized by Kraepelin (1895; 1899a).

ida + Uropygi) as the sister-group to the Araneae. As mentioned above, Dunlop & Horrocks (1996) presented a different scenario.

AMBLYPYGI

Amblypygi—commonly known as whipspiders—are flattened creatures with multi-segmented, extremely long front legs that act as tactile organs. Whipspiders are primarily restricted to the tropics where they most commonly occur in rainforests. Several troglobitic and troglophilic species are known (Weygoldt 1994), some of which display typical cave-dwelling facies with loss of pigmentation, elongate appendages, and the reduction or loss of eyes.

The first amblypygid, *Phalangium reniforme* Linnaeus 1758, was based upon a specimen from "America." Only a few further species were named until the middle of the 19th century, when many species and genera were described by A.G. Butler, K. Kraepelin, R.I. Pocock and others. The fluctuating numbers of species recognized in the 1890's (Fig. 8) was largely based upon the large number of synonymies instituted by Kraepelin (1895, 1899a). Many of these synonymies have not been supported by later workers (e.g. Quintero 1981) and much revisionary work is needed to untangle the calamitous taxonomic state of some genera. Despite the legacy left by Kraepelin's synonymies, new species have been consistently described over the past 100 years, and the current total of 136 described species will surely continue to climb as further genera are examined in detail.

Weygoldt (1996a) presented a detailed cla-

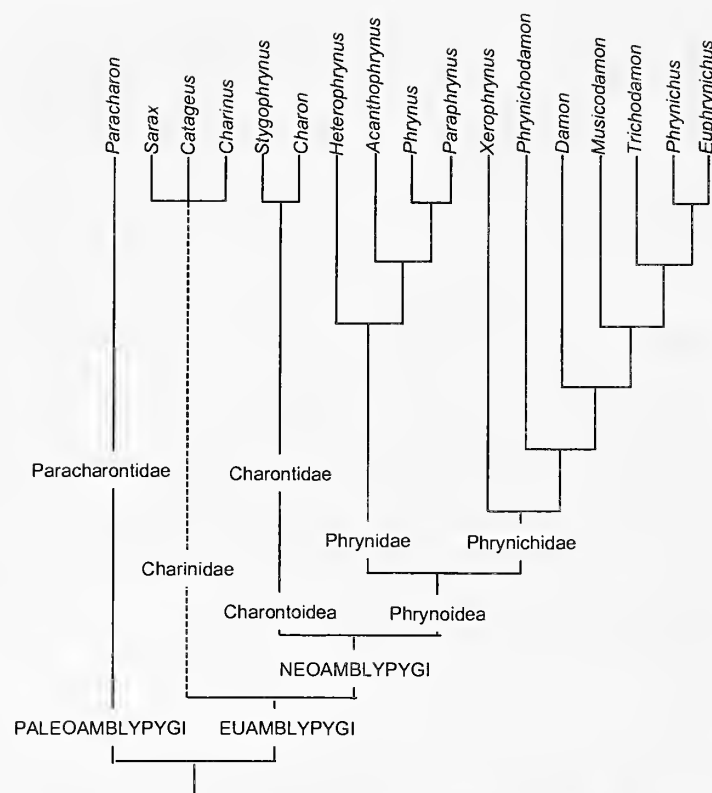


Figure 9.—Relationships between the Recent genera of Amblypygi, redrawn from Weygoldt (1996a, 1996b).

distic analysis of amblypygid genera and proposed a new classification that encompassed five families divided between two suborders, Paleoamblypygi and Euamblypygi. The Paleoamblypygi are represented by a single curious species, *Paracharon caecus* Hansen 1921 (Paracharontidae), which was taken from a termite nest in Guinea-Bissau (Hansen 1921). Its position as the sister-group to the remaining Recent amblypygids (Weygoldt 1996a, and Fig. 9) makes it the only monotypic arachnid suborder in existence, and its isolated and archaic nature is highlighted by a suspected relationship with the four known Carboniferous species (Weygoldt 1996a).

Euamblypygi are represented by four families with varying distributions. The Charinidae is the most widespread family and occurs in most tropical regions of the world; it consists of one circum-tropical genus (*Charinus* Simon 1892), and two genera restricted to south-east Asia (*Catageus* Thorell 1889 and *Sarax* Simon 1892). Weygoldt (1996a) was unable to establish a monophyletic origin for the Charinidae, and further work is needed to determine the species relationships. The Charontidae (*Charon* Karsch 1879 and *Stygophrynus* Kraepelin 1895) are endemic to Australasia, ranging from Burma to the Solomon Islands and northern Australia. The Phrynichidae are found in Africa to south-east Asia

(*Damon* C.L. Koch 1850, *Euphrynichus* Weygoldt 1995, *Musicodamon* Fage 1939, *Phrynichodamon* Weygoldt 1996, *Phrynichus* Karsch 1879 and *Xerophrynus* Weygoldt 1996), with a single outlying genus in Brazil (*Trichodamon* Mello-Leitão 1935). The Phrynidae (*Acanthophrynus* Kraepelin 1899, *Heterophrynus* Pocock 1894, *Paraphrynus* Moreno 1940 and *Phrynus* Lamarck 1801) range from the southern U.S.A. to northern Brazil, although the recent discovery of a member of the genus *Phrynus* from Indonesia (Harvey 2002) raises the prospect of a much wider distribution pattern for the family.

Important papers on amblypygid systematics and taxonomy include Kraepelin (1895), Mullinex (1975), Quintero (1981, 1986), Simon (1892) and Weygoldt (1996a, 1998b, 1999a, 1999b). A comprehensive review of amblypygid morphology, behavior and systematics was recently provided by Weygoldt (2000). The Amblypygi are usually regarded as the sister-group to the Uropygi + Schizomida, thus forming the taxon Pedipalpi (e.g. Shultz 1990), but Weygoldt & Paulus (1979b) placed them as the sister-group to the Araneae.

SCHIZOMIDA

The first Schizomida were described by O. P.-Cambridge (1872) from specimens collected in Sri Lanka. They are small creatures—generally less than 5 mm—with long, tactile anterior legs, and the ability to move very rapidly over short distances. They generally occur in rainforest leaf litter although many species have been described from caves. Others have been accidentally transported with humans, appearing in hot-houses and other environments with constant high humidity. Schizomids possess a peculiar form of sexual dimorphism in which the flagellum of the male is enlarged into a bulbous, unsegmented structure, whereas the segmented female flagellum is unexpanded. Cambridge's (1872) description of the Sri Lankan material treated the male and female specimens as different species—appropriately termed *Nyctalops crassicaudatus* O.P.-Cambridge 1872 and *N. tenuicaudatus* O.P.-Cambridge 1872—until the error was detected. It has since been established that the male flagellum is gripped by the female during courtship (Sturm 1958) and

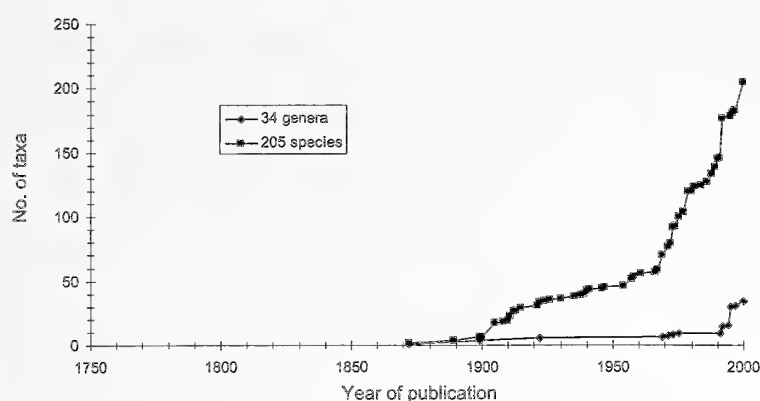


Figure 10.—Numbers of valid Recent schizomid genera and species. Note the rapid increase of new species since 1970, and new genera since 1990.

presumably serves a role in species recognition.

Schizomids are a reasonably uniform group in which, until recently, only a handful of genera and species were known. Until the mid-1980's the majority of species were placed in either *Schizomus* Cook 1899 or *Trithyreus* Kraepelin 1899, but redescription of the type species of each genus by Reddell & Cokendolpher (1984, 1991), allowed for a more reasonable taxonomic break-up of the order. Harvey (1992a) revised the Australian fauna and dispensed with the notion that the majority of schizomids could be included in a few genera, as the level of variation, particularly of the female genitalia, was found to be a useful and significant tool in separating distinct groups of species into genera. Reddell & Cokendolpher (1995) revised the world fauna, described a further 15 genera and removed several older names from synonymy. Additional genera have since been described by Reddell, Cokendolpher, Harvey and their co-workers. To date there are 34 genera of schizomids placed in two families, Protoschizomidae and Hubbardiidae. Twenty-three of these genera have been described since 1990 (Fig. 10) and many more are to be expected once the Asian and African faunas, which have not yet been studied in detail, are considered. Over 180 species have been described, 72% of these since 1960. I expect that over 500 species will eventually be recognized world-wide, as the discovery of new taxa in the Australasian region alone (Harvey, unpublished data) continues. Indeed, since my 1992 revision in which 26 species were recognized (Harvey 1992a), a further 45 new species have been detected, and every new sample seems to contain further species (Harvey 2000, 2001). Cokendolpher & Red-

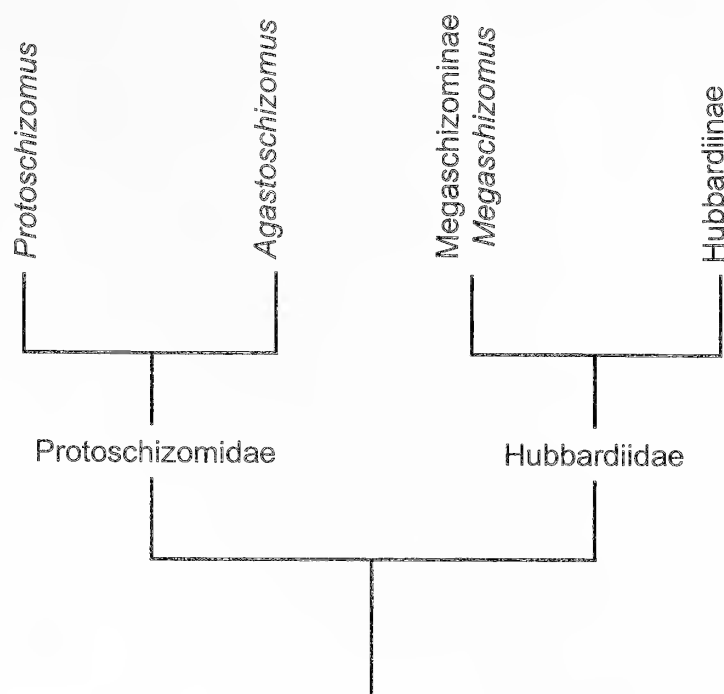


Fig. 11.—Relationships amongst the Schizomida, redrawn from Cokendolpher & Reddell (1992).

dell (1992) presented a cladistic analysis of the Schizomida (Fig. 11), and showed that both families are monophyletic. The fossil record is scant, with three Tertiary genera placed in either the Hubbardiidae (*Calcoschizomus* Pierce 1951 and *Onychothelyphonus* Pierce 1950) or Calcitronidae (*Calcitro* Petrunkevitch 1945). Little can be deduced from the morphology of these Tertiary species, as the preservation is generally poor, and any comparison with modern representatives is extremely difficult.

The Schizomida are strongly confirmed as the sister-group of the Uropygi, but Uropygi + Schizomida are either treated as the sister-group to the Amblypygi (Shultz 1990) or as the sister-group to the Amblypygi + Araneae (e.g., Weygoldt & Paulus 1979b). Important papers on the systematics of schizomids are Hansen & Sørensen (1905), Lawrence (1969), Rowland & Reddell (1979a, 1979b, 1980, 1981), Harvey (1992a), Cokendolpher & Reddell (1992) and Reddell & Cokendolpher (1995).

SOLIFUGAE

The Solifugae, sometimes called sun-spiders, wind-scorpions or camel-spiders, are some of the most spectacular arachnids and are equipped with large, powerful, two-segmented chelicerae. Adults range in size from 1–7 cm. They can be easily distinguished from other arachnids by the presence of malleoli (racquet organs), the peculiar, stalked

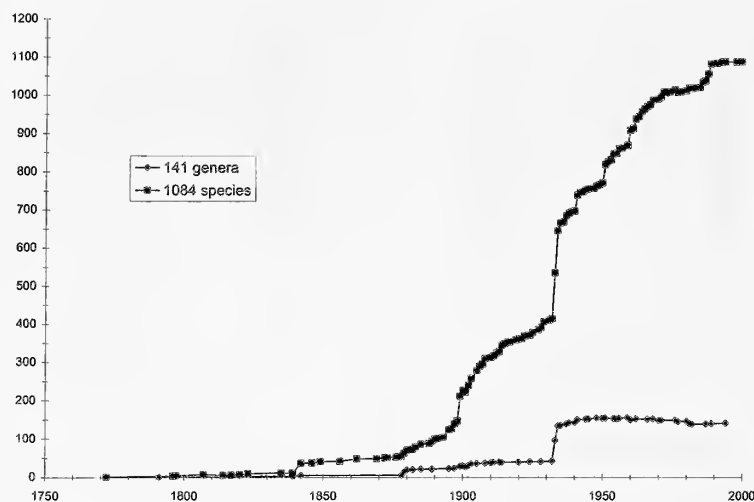


Figure 12.—Numbers of valid Recent solifuge genera and species. Note the marked increase in described genera and species during the 1930's, which was largely the work of one worker, C.F. Roewer.

structures situated on the ventral surfaces of leg IV.

Although solpugids were known to pre-Linnean scholars, the first solpugid was officially described as *Phalangium araneoides* Pallas 1772. Lichtenstein (1796) and Lichtenstein & Herbst (1797) added four new species that were placed in the first genus dedicated to the group, *Solpuga* Lichtenstein 1796. Early attempts at producing a classification of the order were attempted by C.L. Koch (1842), Simon (1879) and Kraepelin (1899b), but the modern classification was established by Roewer (1932, 1933, 1934) who instigated a new classification and described numerous new genera and species (Fig. 12). Roewer's reliance upon a small set of character systems to distinguish between genera or subfamilies has been critically challenged by numerous workers (e.g. see Muma 1976) and it is clear that the current classification is severely flawed at many levels. Much work must be undertaken to even begin to sort out the confusion. The only regional fauna which is in relatively good condition is that of the New World, where Roewer had little impact, and where later researchers such as Muma and Brookhart (e.g. Brookhart & Muma 1981, 1987; Muma 1951, 1970, 1971; Muma & Brookhart 1988) and Maury (e.g. Maury 1982, 1985, 1987) have been able to formulate a worthwhile classification based upon a synthesis of many characters.

Solifugae currently consists of 12 families, 141 genera and 1,084 species (Table 1). No attempt has been made to group the 12 fam-

ilies into superfamilies and the current classification is a flat structure devoid of any phylogenetic signal. The Rhagodidae seem to stand apart from the remaining Solifugae in a number of ways and Roewer (1934) depicted them as separate from other families. However, the systematic position of this family has not been empirically tested, and a phylogenetic study of the Solifugae would allow testing of morphological and behavioral traits.

Three species have been described from fossils, and each is placed in a monotypic genus: *Protosolpuga carbonaria* Petrunkevitch 1913 (Protosolpugidae) from the Pennsylvanian (Carboniferous) of Mazon Creek, U.S.A., *Happlodontus proterus* Poinar and Santiago-Blay 1989 (Ammotrechidae) from Miocene-Eocene Dominican Amber and *Cratosolpuga wunderlichi* Selden 1996 (Ceromidae) from the Aptian (Lower Cretaceous) of Brazil.

The Solifugae are commonly accepted as the sister-group to the Pseudoscorpiones, and both are placed in the clade Haplocnemata (e.g. Shultz 1990; Weygoldt & Paulus 1979b).

Important publications include Simon (1879), Kraepelin (1899b), Roewer (1932, 1933, 1934), Birula (1938), Muma (1951, 1976), Lawrence (1955), Selden & Shear (1996) and Punzo (1998).

PSEUDOSCORPIONES

Pseudoscorpions are small predatory arachnids, which superficially resemble scorpions, but that lack the elongate metasoma (tail) and telson (sting) characteristic of the latter group. The resemblance is mostly due to the enlarged pedipalps that in both groups are modified with the tarsus inserted ventrally under the tibia to form a chelate appendage. Adults range from less than 1 mm to 1 cm in length.

The first pseudoscorpions were described by Linnaeus (1758) who named *Acarus cancroides* Linnaeus 1758 from Europe and *Acarus scorpioides* Linnaeus 1758 from Surinam—ironically the three names he used linked the group to mites (*Acarus* Linnaeus 1758), crabs (*cancroides*) and scorpions (*scorpioides*), indicating a distinct uncertainty of their relationships! Geoffroy (1762) quickly realized that *A. cancroides* was misplaced among the mites and erected the inaugural generic name, *Chelifer* Geoffroy 1762.

All pseudoscorpions were placed in a single family until 1892 when the young Italian bi-

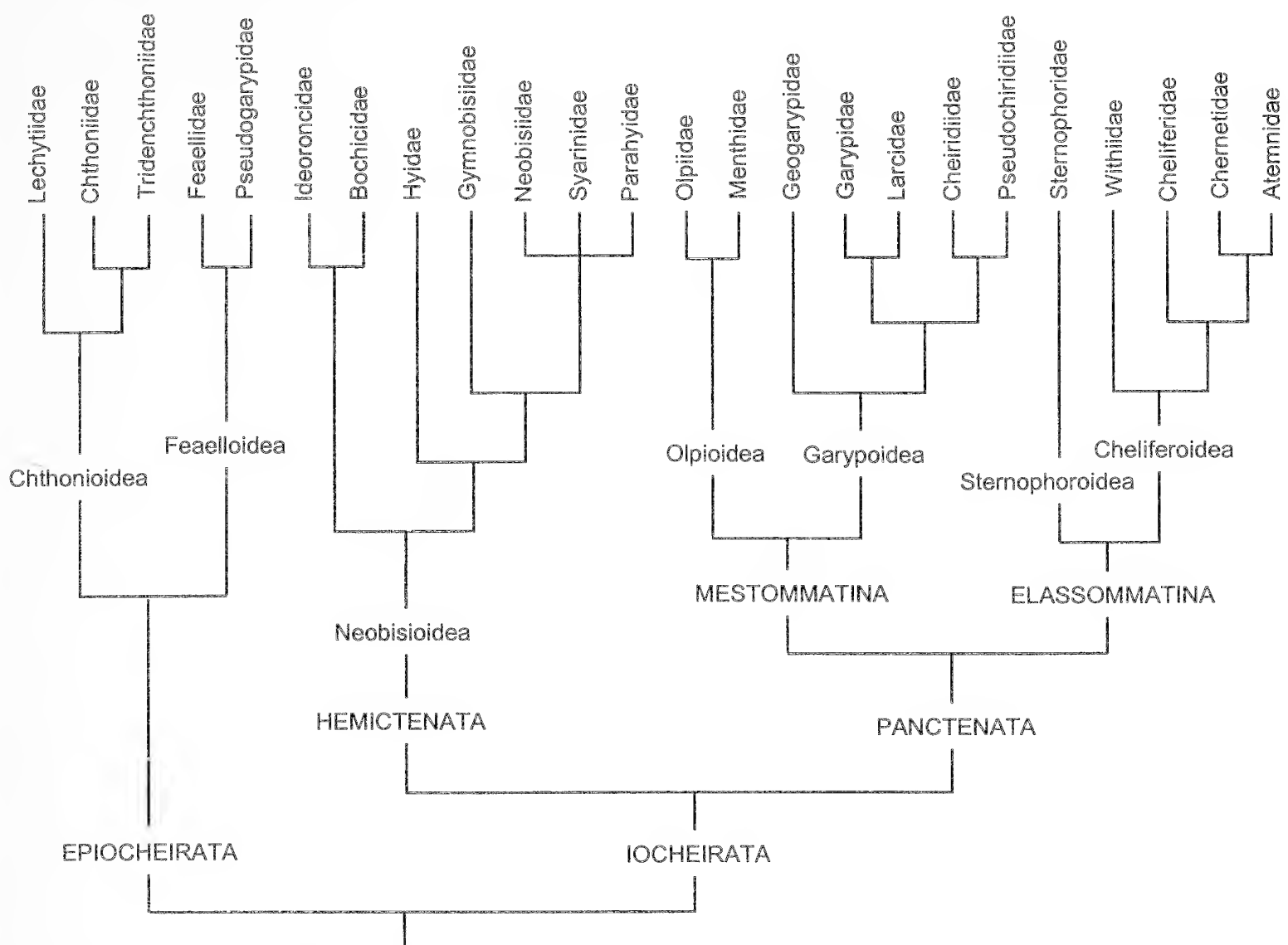


Figure 13.—Relationships amongst the Pseudoscorpiones, redrawn from Harvey (1992b).

ologist L. Balzan produced a novel classification in which the order was divided into two suborders—Hemictenodactyli and Panctenodactyli—and four families (Balzan 1892). Chamberlin (1929, 1930, 1931) produced a different classification that remained largely unchanged for over 60 years, despite minor modifications by Beier (1932a, b) and others. Harvey (1992b) provided the first comprehensive cladistic treatment of the order (Fig. 13) and recognized two suborders—Epiocheirata

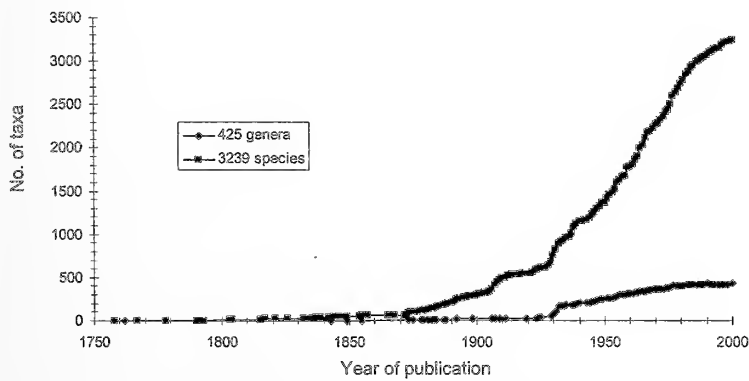


Figure 14.—Numbers of valid Recent pseudoscorpion genera and species. Note the steady increase in described species since the 1930's.

and Iocheirata—each based on several autapomorphic characters. These include the presence (Iocheirata) or absence (Epiocheirata) of a venom apparatus in the chelal fingers, and the presence (Epiocheirata) or absence (Iocheirata) of the accessory trichobothrium *xs* and coxal spines. Among several changes to the previous classifications, Harvey (1992b) transferred the Cheiridiidae and Pseudochiridiidae, which until then had been combined with the Sternophoridae in the Cheiridioidea (e.g. Chamberlin 1931), to the Garypoidea. Judson (2000) has recently questioned the position of these two families and reinstated the Cheiridioidea for the Cheiridiidae and Pseudochiridiidae.

Over 3,200 species in 425 genera are currently recognized and the discovery of new species and genera continues unabated (Fig. 14), even in well-studied areas such as North America. The number of Recent families currently stand at 24 (Harvey 1992b), but the systematic position of several unusual groups currently included within other families may expand this number.

Until recently, the fossil record solely consisted of Tertiary species embedded in amber from the Baltic, Caribbean or Burma, with most species placed in Recent genera. The discovery of Cretaceous pseudoscorpions (Schawaller 1991; Whalley 1980) and most importantly, the description of *Dracochela deprehendor* Schawaller, Shear & Bonamo 1991 from the Devonian of New York, has firmly established that the order is an ancient clade that moved into terrestrial environments some time prior to 380 MBP. Harvey (1992b) treated *Dracochela* Schawaller, Shear & Bonamo 1991 as a member of the suborder Epiocheirata, although certain morphological features are not sufficiently preserved or visible on the specimens to enable the placement within the group to be tested with certainty. Important publications include Chamberlin (1931), Beier (1932a, 1932b), Muchmore (1990), and Harvey (1991, 1992b).

DISCUSSION

The somewhat provocative title of this paper is not intended to scorn those arachnologists who focus upon the mega-diverse groups. Indeed, the challenges faced in documenting and understanding the enormous diversity of the Acari and Araneae (Halliday et al. 2000; Platnick 1999) far outweigh the problems faced by researchers dealing with the smaller arachnid orders. Nevertheless there is still much to be gained from a more coordinated and detailed examination of the phylogeny and diversity of the other orders. New species are constantly being found in most groups, new characters are being discovered which are helping to refine and challenge previous classifications and the use of cladistic methodology has produced some testable phylogenetic hypotheses. Although some orders have been the subject of detailed phylogenetic analysis (i.e., Amblypygi, Schizomida and Pseudoscorpiones), others have yet to be examined empirically, and none have been the subject of combined molecular and morphological treatments such as that recently conducted for Opiliones (Shultz & Regier 2001). Such studies are needed to further test the monophyly of purported groups within each order and to provide a judicious phylogenetic framework within which other scientific disciplines can operate.

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THE INFLUENCE OF STARVATION ON DISPERSAL IN THE SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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ABSTRACT. Colonies of the social spider, *Stegodyphus mimosarum*, are philopatric and inbred, with limited dispersal capabilities. Colony founding events by mature males and females have been observed periodically. We set out to test the influence of food on the spiders' readiness to leave a colony. Thirty colonies (40 spiders in each) were established under laboratory conditions and confined within netting. For 31 days, 15 colonies were fed daily *ad libitum*, so that the mean amount of food available was greater than the mean requirements of the colony. The other fifteen colonies were starved. The netting was then removed, permitting emigration and movement from colonies was noted for two weeks. Following risk sensitivity theory, we expected more spiders to leave the unfed colonies due to starvation. However, a significantly higher absolute number of spiders left colonies where food was abundant. While fewer spiders left unfed colonies, more of these spiders died, such that the relative number of spiders remaining at the end of the trial was not significantly different between treatments. Even when they were starved, the decision to leave a colony was not based on a lack of food. Low food availability increased mortality, yet it did not alter the remaining spiders' decision to move. Therefore the decision to move is based on factors beyond prey availability, which may include the state of maturity of the spiders, the motivational state, the high cost of migration and reserves.

Keywords: Colony founding, food availability, risk sensitivity

Stegodyphus mimosarum Pavesi 1883 and *S. dumicola* Pocock 1898 are social spiders that inhabit dry thornbush country in southern Africa (Kraus & Kraus 1988). The life cycle, growth rate and seasonal development of *S. mimosarum* are discussed elsewhere (Crouch & Lubin 2000; Seibt & Wickler 1988a & b).

The low genetic diversity of social spider colonies, (Johannsen & Lubin 1999; Smith & Engel 1994) together with their characteristically patchy distribution, is an indicator of poor dispersal capabilities (Henschel et al. 1995). Further, the high cost associated with dispersal greatly reduces the chances of successful emigration (Crouch et al. 1998; Seibt & Wickler 1988a). Most dispersal has been observed over relatively short distances, i.e., from 1–26 m (Henschel et al. 1995 in *S. dumicola*). However, distances between patches of nests of *S. mimosarum* (and *S. dumicola*) are beyond the spiders' walking range (Seibt & Wickler 1988a), which suggests that additional methods of dispersal exist. Periodic dispersal events have been observed (Crouch et

al. 1998; Seibt & Wickler 1988a) and raised new questions about emigration. Dispersal events seem to be infrequent; dependent on the state of maturity of the spiders (Crouch et al. 1998), the season (Crouch & Lubin 2001), and on specific environmental conditions, e.g., strong, gusty winds (Crouch et al. 1998).

However, even for poor dispersers, when resources in a particular area become depleted, the animals face extinction if they do not leave and find another location before the resources are completely exhausted. Ultimately, most animals disperse to obtain more food or space, such as soon after juveniles are born / hatch out (founder hypothesis), or to escape predation, starvation or high parasite loads (escape hypothesis) (Decae 1987). For spiders, the proximate reasons driving the decision to disperse include access to resources (Ward 1986), the season (wind, temperature) (Crouch & Lubin 2001), and the size of the animal (Miller & Miller 1991). In addition, the developmental stage of the animal (most spiders disperse as juveniles) (Foelix 1996),

its internal state of readiness (e.g., mature males and females) (Seibt & Wickler 1988a) are contributing factors.

Access to resources may be influenced by the mean long-term rate of food available and by variation in intake (Milinski & Parker 1991). Variability in access to resources may be influenced by time, season, position and intra-group competition, so that some spiders obtain a higher quantity of food than others. Consequently, there would be a range of spider sizes within the retreat (Ulbrich et al. 1997; Ward 1986). The influence of variability in access to resources on dispersal was examined in a previous experiment. We found no significant increase in the number of spiders leaving with increasing group size (Bodasing et al. 2001). The mean amount of food obtained by each colony is influenced by nest location (Biere & Uetz 1981), prey availability (Miyashita 1991; Schneider 1996) and season (Crouch & Lubin 2001). Indeed, the mean amount of food obtained per spider determines spider size and hunger levels (Miyashita 1991). In social spiders, the mean quantity of food obtained per spider decreases with increasing group size, so that spiders are ultimately smaller in larger nests (Reichert et al. 1986; Ward 1986). This should have an impact on adult spider size and the time of maturity, so that spiders in nests where the mean amount of food available is less than their mean caloric requirements would reach a smaller adult size, or would mature later. Low levels of resources would ultimately affect reproductive capacity (Schneider 1995). The short-term consequence of reduced spider size may be dispersal (Miyashita 1992). Dispersal would be expected to spread the risk of starvation in related groups, since dispersing spiders may obtain more food (Kuno 1981), while remaining could lead to starvation.

Food resources have been proposed as a proximate stimulation for dispersal in spiders. We test this mechanism in this paper, focusing primarily on a risk sensitive foraging approach. Dispersal decisions have been explained by using risk-sensitivity (Caraco & Gillespie 1986; Uetz 1988). If an individual is meeting its current and long term requirements, remaining at the present site reduces the risk of starvation by reducing the variance in food intake (i.e. foraging in a risk-averse manner). However, when current resources are

fewer than the individual's requirements (i.e. the mean food intake is lower than the long-term requirements) there is a negative energy budget. It is then preferable to move to improve the chance of obtaining resources (i.e. foraging in a risk-prone manner) (Caraco & Gillespie 1986; Uetz 1988).

We tested whether differences in mean feeding rates influenced the decision of *S. mimosarum* to disperse. Colonies of the same size were subjected to one of two treatments: an abundance of food or an absence of food. This created two types of colonies: some where individuals were meeting their long term requirements (risk-averse foragers) and others, where individuals were not meeting their long term or short term energy requirements (risk-prone foragers). If food resources are a stimulus to disperse, and if risk sensitivity is a mechanism, then risk prone spiders in the starved colonies should adopt a strategy of dispersal, as this should increase their chances of obtaining food and eventually reaching maturity, whereas staying could result in delayed maturation, starvation and possibly death. Specifically, we predicted that more spiders would disperse from starved colonies.

METHODS

Nests of *Stegodyphus mimosarum* were collected from Ashburton, KwaZulu-Natal, South Africa (24° 40' S, 30° 27' E) in March, October and December 1999, and maintained at the School of Life and Environmental Sciences, University of Natal, Durban, South Africa. This provided three complete replicates of the experiment. For two weeks, the spiders were allowed to acclimate. During this time, they were kept under controlled conditions, at 28 °C, and on a 12 /12 light-dark cycle to remove the influence of day length. The spiders were fed a diet of adult mealworms, *Tenebrio molitor*, and mist-sprayed with water once a week. Spiders were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1000 mm diameter and 500 mm or 1000 mm high). Each cage had a removable wooden base supported by a metal stand. The stand was immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed access for feeding.

In *S. mimosarum*, the size of spiders was smaller in larger nests (Ward 1986) and it is

expected that optimum spider size would be reached in nests of less than 40 spiders (Siebt & Wickler 1988a). We therefore used colonies of 40 spiders for the experiment. During each trial, spiders were removed from their field nests and allocated to ten colonies of 40 spiders each. All spiders used in these trials were juveniles. Each colony contained six large, 26 medium and eight small spiders. However, the size categories were altered in accordance with the sizes of spiders available for each trial. In any single trial, the size distribution between treatment groups (fed and unfed) and among individual colonies was equitable.

Colonies were weighed on a Mettler AE 240 balance and their masses were compared. Each colony mass was adjusted by including spiders of different sizes so that all ten colonies were similar in mass (within 0.1 g), and the colonies were re-weighed. The starting mass of each colony was therefore constant within each trial (10 colonies). The mean spider mass was calculated from the mass of the colony (colony mass divided by 40). A subsample of spiders (15–17 individuals) from each colony was measured (total body length and prosoma width) and mean body length and mean prosoma width were calculated for each colony. Individuals within each colony were color-coded with a combination of two colors (unique to each colony) of water-based poster paints, applied to the dorsal surface of the abdomen, so that the colony origin of moving spiders could be recorded.

Forty-nine *A. robusta* plants (600 mm to 700 mm high) were potted in plastic pots (base diameter = 180 mm, top diameter = 240 mm and height = 205 mm). Each plant was trimmed of all but two or three branches, none of which overhung the pot rim. The plants were arranged in the experimental room, in a grid of seven rows, each row with seven plants. The pot centers were 560 mm apart in each row and approximately 820 mm apart diagonally.

The windowless experimental room was artificially lit with 14 “daylight” incandescent bulbs of 100 watts each. These were mounted on a metal frame suspended from the ceiling. A timer controlled the 12 hour light/dark cycle, which removed the effect of changing day length during different trials. Nests were randomly allocated to plants. However, no nests were placed on the plants nearest the walls to

prevent any edge effect from the proximity of the walls. Each colony was enclosed within a bag made of fine netting, and was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. The top of each bag had an opening, tied with string, through which the spiders were fed and the prey remains removed. The colonies were left for four days to start building a retreat and capture web (Day 1–Day 4).

Five colonies were randomly allocated to each treatment; either fed for a total of 31 days, or unfed. The feeding treatment consisted of four adult mealworms daily. The bags with the unfed colonies were opened and retied daily to create the same amount of disturbance as that experienced by the fed group. All colonies were mist sprayed with water once weekly. After 20 days (Day 5–Day 24) of this treatment, the spiders were removed from the bags and dead spiders were discarded. Those spiders that had molted were re-painted. The mass of each colony was again measured, and compared with the initial colony mass in each trial. Any missing spiders were replaced from a separate additional source of fed and unfed spiders, which had been housed under the same conditions as the ten colonies. Colonies were weighed again, and the mean spider mass was calculated.

We could not bring the colony back to the original number (40) in all trials, due to the constraints of the number of spiders required for each trial (400 plus extras). Under these circumstances, when we replaced spiders, priority was given to missing individuals first and then secondly to dead ones. The final number was as close to 40 as possible (Mean \pm S.E = 34.2 ± 3.717). The colonies were returned to the netting bags on trees for four days (Day 24–Day 28) to repair their nests and capture webs. This was followed by another four days (Day 28–Day 31) of the fed/unfed regime within the bags. The bags were then carefully removed with as little damage to the capture web as possible. On Day 31, we could not count, measure or reweigh the colonies before the commencement of the observations, as this required taking apart the nest again and further disturbance of the nest and spiders. We therefore used the mean spider mass from Day 24 as the starting point of

the observations, although the treatment continued for another week after this (Day 31).

Daily observations were made on all movements of spiders for the next fourteen days (Day 32–Day 45). No further feeding occurred during this period, but the nests were mist-sprayed once weekly. Each tree or colony was examined for spiders and/or silk. Any spiders within a retreat were left undisturbed, although occasionally the retreat was thin enough to estimate of the number of spiders present. Information was recorded on the source of the spiders based on color, the number of spiders emigrating and where they were finally found. We recorded the total number of spiders moving from each colony, the number left behind and the number missing and/or dead. We calculated the number leaving divided by the total number in the colony on Day 24. These proportions were not normally distributed and all relative numbers were $\sqrt{\text{arcsine } x}$ transformed. Data were analyzed by ANOVA (assumptions verified), Wilcoxon Signed Ranks Tests and Mann-Whitney U-tests as appropriate, using SPSS version 9.0 for Windows. Voucher specimens were deposited at the Durban Natural Science Museum.

Each experiment (five fed and five unfed colonies) was repeated three times: February–April 1999 (late summer/autumn), October–December 1999 (spring/summer) and January–February 2000 (mid/late summer). The total sample was therefore fifteen fed and fifteen unfed colonies. The trials presented reflect activity during the summer months when spiders are juveniles, subadults and adults. Although adult spiders were observed emigrating, in our experiments the spiders used were all either juvenile or subadult. This was done to remove the confounding effect of maturity, so that only the availability of food differed between treatments.

RESULTS

At the start of each trial, we ascertained that there were no significant differences in mean body length (Fig. 1a), mean prosoma width (Fig. 1b) or mean mass (Fig. 1c) between spiders in the two types of treatment (ANOVA: $F_{1,9} < 3.470$, $P > 0.100$ in all cases). Spiders were significantly smaller during Trial 2 (October 1999) compared with the other trials (Figs. 1a, b & c).

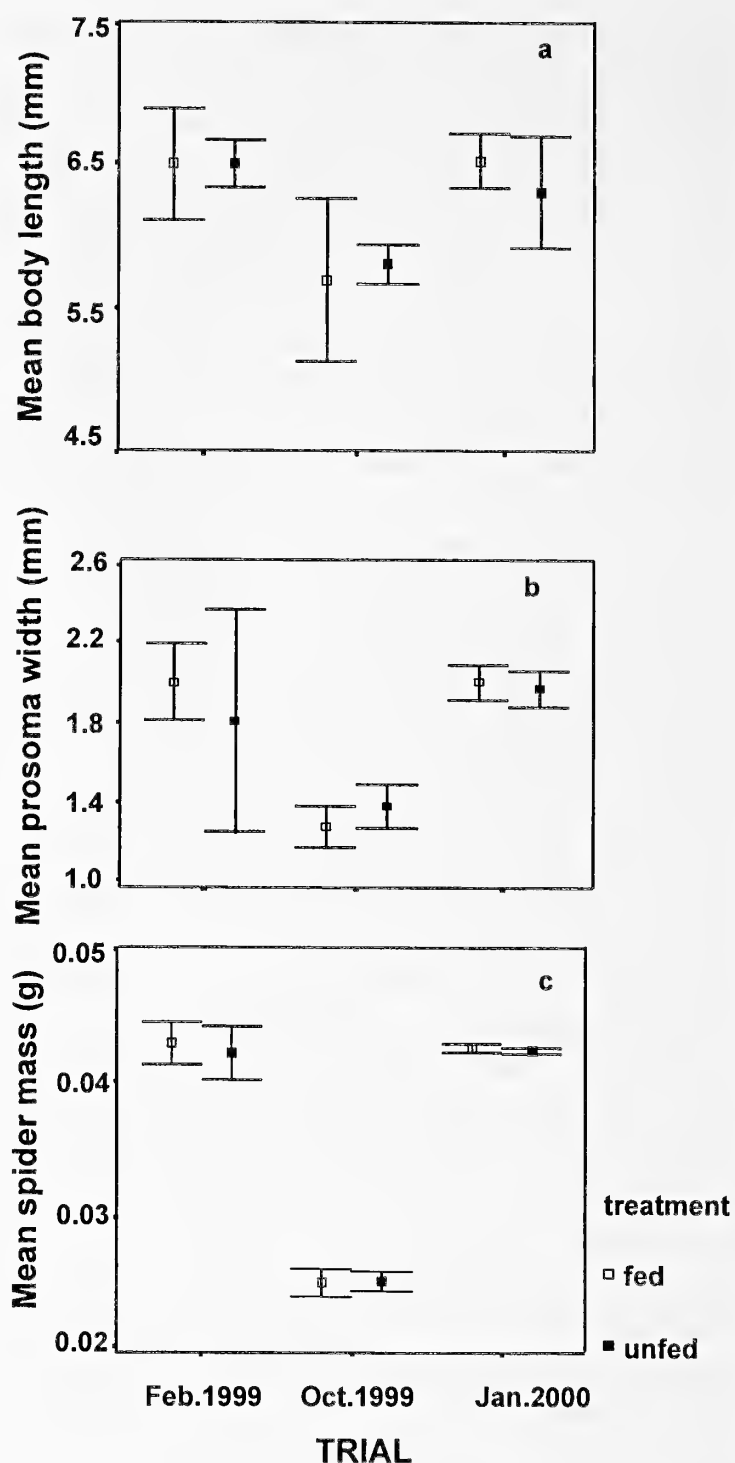


Figure 1.—Comparison of spider size in the fed and unfed groups at the start of each trial. We present the mean body length (a), mean prosoma width (b) and mean mass (c) of spiders \pm 95% confidence limits. There was no significant difference in spider size (body length, prosoma width and mean mass) between treatments (ANOVA $F_{1,9} < 3.470$, $P > 0.1$ in all cases). $n = 5$ colonies of 40 spiders in each category. Note that spiders were smaller during the October 1999 trial.

On Day 24, fed colonies were significantly larger than the unfed colonies, (Mann Whitney U-test on colony mass: Trial 1: $Z = -2.611$, $P = 0.009$, Trial 2: $Z = -2.402$, $P = 0.016$, Trial 3: $Z = -2.611$, $P = 0.009$). Moreover, in the fed colonies, tunnels opening onto the lower surface were visible in the retreats and capture web showed signs of recent maintenance with fresh silk extending onto

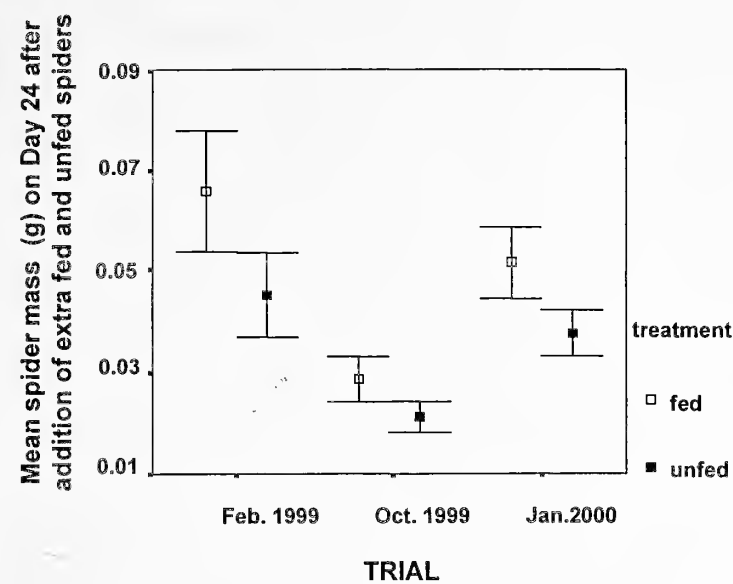


Figure 2.—Spider size (Mean \pm 95% confidence limits) after differential feeding and before dispersal. Comparison of the mean mass of spiders in the fed and unfed groups on Day 24 of each trial. Spiders were significantly larger in the fed groups (except in Trial 2; see text for statistical analysis). $n = 5$ colonies for each mean.

the netting. Spiders were significantly heavier (higher mean spider mass) in fed colonies than in unfed colonies (Mann Whitney U-test: Trial 1: $Z = -2.611$, $P = 0.009$, Trial 2: $Z = -1.984$, $P = 0.047$, Trial 3: $Z = -2.611$, $P = 0.009$) (Fig. 2). The unfed spiders were already experiencing the consequences of a lack of resources after 24 days. They were smaller in size (mean spider mass) and were not able to repair their retreats adequately after nests were taken apart on Day 24. A little fresh silk held the retreat together, and only a few tunnels were observed. There was generally very little capture web. Furthermore, the unfed colonies experienced a higher mortality than fed spiders. This is incompatible with reports that *S. mimosarum* kept for three to six months without food and water survived (Steyn 1959).

After adding in the extras, the “new” mean mass on Day 24 was significantly different from the start (Day 0) mass (Mann Whitney U-test: Trial 1: $Z = -2.611$, $P = 0.009$, Trial 2: $Z = -2.611$, $P = 0.009$, Trial 3: $Z = -2.522$, $P = 0.012$). Adding in the extra fed and unfed spiders on Day 24 maintained the overall effects of the two treatments, so that fed spiders were still significantly larger than unfed ones.

We compared the absolute number of spiders moving from all colonies (Fig. 3a), and significantly more spiders left the fed groups

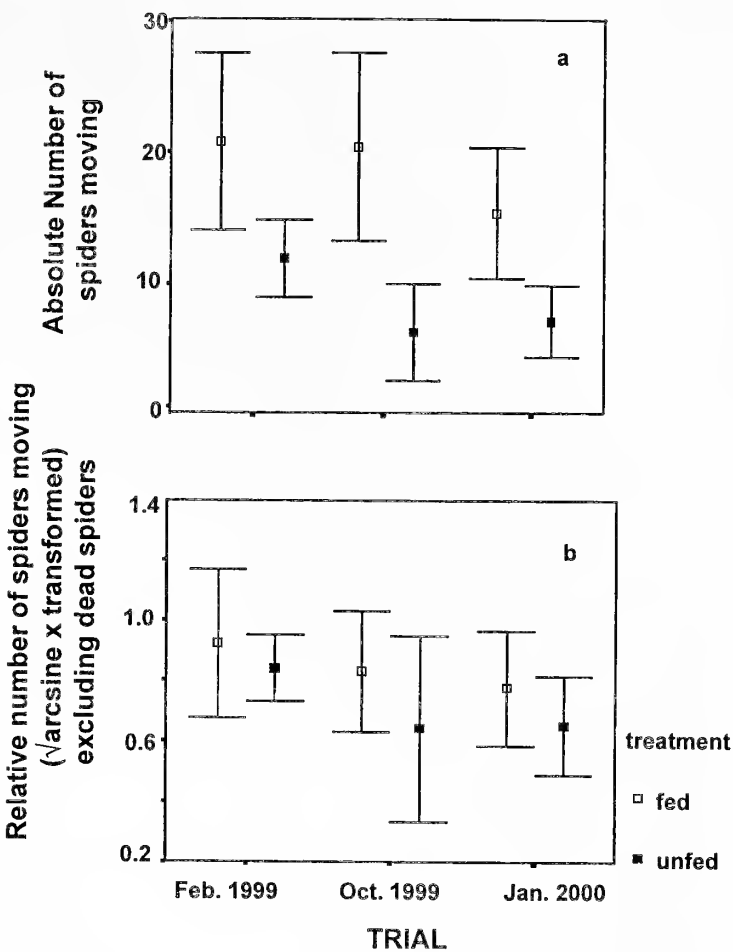


Figure 3.—Dispersal of spiders under different feeding regimes. (a). The absolute number (Mean \pm 95% confidence limits.) of spiders that emigrated from the fed and unfed groups in all three trials. Significantly more spiders left the fed groups than the unfed groups (see text for analysis). (b). Relative dispersal ($\sqrt{\text{arcsine } x}$ transformed) after accounting for dead spiders. There was no significant difference in the relative number of spiders leaving under the fed and unfed treatments in all three trials. $n = 5$ colonies for each mean.

(ANOVA: Trial 1: $F_{1,9} = 11.605$, $P = 0.009$, Trial 2: $F_{1,9} = 23.558$, $P = 0.001$, Trial 3: $F_{1,9} = 16.40$, $P = 0.004$). We also tested the relative number of spiders moving (number moving divided by Day 24 final number of spiders) ($\sqrt{\text{arcsine } x}$ transformed) in each trial. When the relative number of spiders moving was based on the Day 24 total number of spiders per colony, significantly more spiders left the fed colonies (ANOVA: Trial 1: $F_{1,9} = 9.982$, $P = 0.013$; Trial 2: $F_{1,9} = 23.823$, $P = 0.001$; Trial 3: $F_{1,9} = 9.711$, $P = 0.014$). Fed spiders showed a greater propensity to emigrate than the unfed spiders.

However, when the number of dead spiders on Day 45 was excluded from the Day 24 total, the relative number moving ($\sqrt{\text{arcsine}}$ [number moving divided by (Day 24 total minus number of dead spiders on Day 45)], transformed) was not significantly different

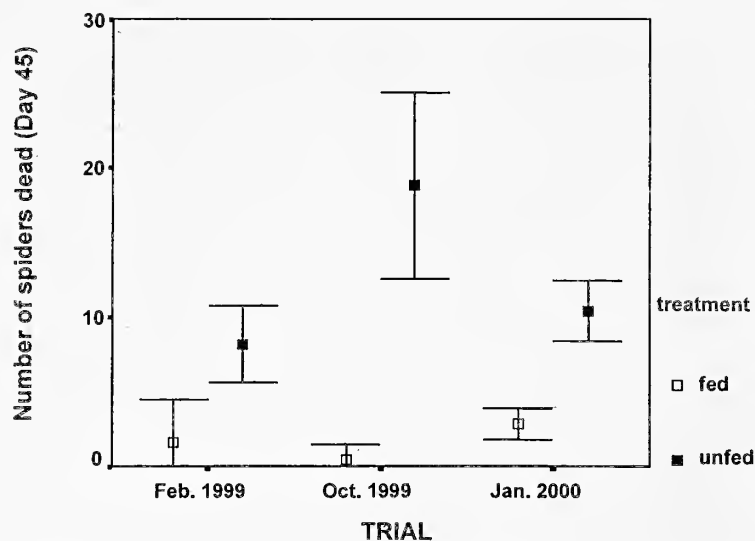


Figure 4.—Mortality under different feeding regimes. Significantly more spiders died in the unfed groups in all three trials (see text for analysis). The number of dead spiders was especially high after the October trial, when spiders were smaller than in the other trials. (Data are Mean \pm 95% confidence limits.) $n = 5$ colonies for each mean.

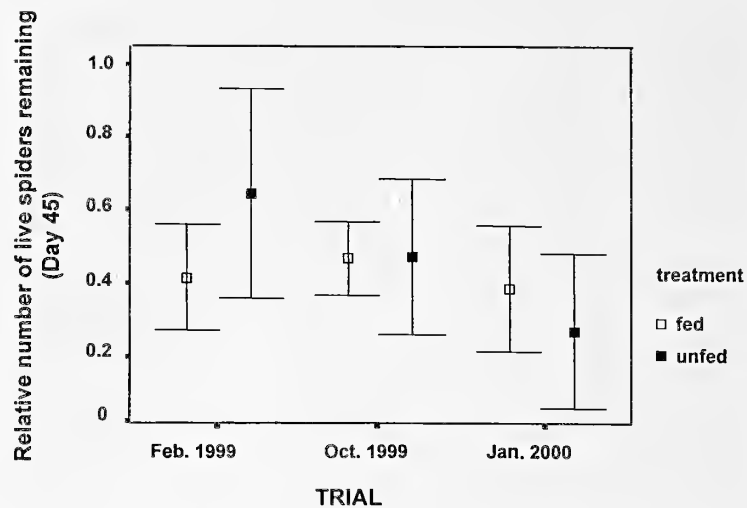


Figure 5.—Relative number (Number left on Day 45 divided by the Day 24 number—the number dead on Day 45) remaining at the end of each trial. There was no significant difference between treatments in the number of spiders remaining at the end of 45 days (see text for analysis). Data are Mean \pm 95% confidence limits. $n = 5$ colonies for each mean.

between treatments (ANOVA: Trial 1: $F_{1,9} = 0.704$, $P = 0.426$; Trial 2: $F_{1,9} = 2.086$, $P = 0.187$; Trial 3: $F_{1,9} = 1.842$, $P = 0.212$; Fig. 3b). This analysis assumes that those spiders were not available to move, i.e., they were effectively dead on Day 24. Under this analysis, the number of spiders leaving the fed colonies was no different from the number leaving the unfed colonies.

The mean mass of the spiders remaining in the nest at the end of each experiment (Day 45) was not significantly different from the mean mass at the start (Day 0), (Mann Whitney U-test: Trial 1: $Z = -1.467$, $P = 0.142$, Trial 2: $Z = -0.940$, $P = 0.347$, Trial 3: $Z = -1.984$, $P = 0.047$). In the fed groups, the spiders that remained were possibly the smaller ones at the start of the trial, or spiders that did not gain mass during the experiment (mass \leq mean mass at the start). In the unfed groups, those remaining could be the spiders that were initially the larger ones (mass of spiders $>$ mean mass) that lost mass during the experiment, but which managed to survive.

By Day 45, significantly more spiders died in the unfed groups than in the fed groups, in all trials (ANOVA: Trial 1: $F_{1,9} = 22.926$, $P < 0.001$; Trial 2: $F_{1,9} = 63.879$, $P < 0.001$; Trial 3: $F_{1,9} = 82.514$, $P < 0.001$) (Fig. 4). Indeed, by Day 24, significantly more spiders died in the unfed groups (ANOVA: Trial 1: $F_{1,9} = 33.923$, $P < 0.001$, Trial 2: $F_{1,9} = 7.149$, $P = 0.028$, Trial 3: $F_{1,9} = 16.794$, $P =$

0.003). This is especially noticeable in the October 1999 trial, when spiders were much smaller than in the other two trials.

The absolute number of spiders left at the end of the experiment was significantly different between treatments in trial 2 (ANOVA: Trial 1: $F_{1,9} = 0.312$, $P = 0.592$, Trial 2: $F_{1,9} = 10.127$, $P = 0.013$, Trial 3: $F_{1,9} = 4.128$, $P = 0.077$). There was no significant difference in the relative numbers of spiders that remained in the colony at the end of the trial (45 days) (ANOVA: Trial 1: $F_{1,9} = 3.959$, $P = 0.082$, Trial 2: $F_{1,9} = 0.003$, $P = 0.957$, Trial 3: $F_{1,9} = 1.399$, $P = 0.271$) (Fig. 5). The number of spiders remaining was therefore not associated with the different treatments, but was influenced by some other factor. This may be due to the trial date (time of year of the trial/season or their size/stage of maturity), since significantly more spiders remained in Trial 2 (October 1999) (ANOVA: $F_{1,29} = 3.857$, $P = 0.034$), when spiders were smaller than in the other two trials.

DISCUSSION

Most spider species are solitary and aggressive. As a result, most spiderlings disperse soon after hatching (Foelix 1996). However in social *Stegodyphus* spp., this is not the case. Spiderlings remain together through to maturity, and several successive generations may remain in the original nest (Seibt & Wickler 1988b). Dispersal over short distances may

occur (sociotomy / budding), or periodic dispersal events, by mature males and females, over short or longer distances may ensue (Seibt & Wickler 1988a; Crouch et al. 1998).

We examined one of the proximate factors influencing the decision to emigrate, i.e., access to resources. The effect of access to resources in a social spider colony may be influenced by the mean quantity of resources available, and by variation in the amount of resources. In a previous experiment (Bodasing et al. 2001), we focussed on the influence of variation in the amount of resources on dispersal. Four colony sizes (4, 16, 32 & 64) were set up under a proportional feeding regime. Variance in spider size occurred due to intra-group competition. We expected this variance to be greater and to trigger dispersal in larger colonies, but there was no significant increase in the number of spiders leaving with increasing group size (Bodasing et al. 2001). In the current experiment, some colonies had a mean amount of food available greater than the mean requirements of the colony, and other colonies had a mean amount of food less than the mean amount required by the colony. Those spiders deprived of food would have fewer reserves. If spiders were responding to risk, we expected starving individuals to relocate to find an alternate nest site where they may find food. However, significantly more spiders moved from the fed groups in all three trials (absolute number and relative number based on Day 24 total), while the unfed spiders adopted a risk-averse foraging strategy.

In some spiders, the costs of relocation may be high. There is a cost to silk production (Tanaka 1989; Reichert et al. 1986), the danger of predation either during moving or rebuilding (Vollrath 1985, Reichert et al. 1986, Sundstrum 1994) and the reduced chance of finding a mate (Seibt & Wickler 1988a). These dispersal costs must be compared to the costs of not dispersing, including the cost of inbreeding, which characterizes social spider communities (Johannsen & Lubin 1999). There is also a smaller adult spider size in larger colonies (Reichert et al. 1986; Ward 1986), which would ultimately affect reproduction (Schneider 1996). The costs of smaller size may be countered by prolonged development, rather than building a new web (Vollrath 1985). Even in the fed groups, those remain-

ing were the smaller spiders. These spiders possibly lacked the resources to relocate.

Females may not be able to accumulate sufficient resources to reproduce if they remain in the initial colony, but predation may be higher on migrating individuals. Higher predation during emigration is reported for *Aneides eximius* Keyserling 1884 (Christenson 1984). Increased web site relocation may make a spider more prone to predation. Vollrath (1985) reports up to 90% mortality of *Nephila* (males) travelling long distances between webs. Furthermore, information about the new site will not be available without an investment of resources and time and it may not be possible to return to the old site (Vollrath 1985). These costs associated with moving may be more than the costs of smaller size and longer development (Vollrath 1985). In addition, Anderson (1974) points out that many adult spiders may survive starvation by reducing their metabolic rate. Some spiders may also switch to using fat as a catabolic substrate (Tanaka & Ito 1982). It may be preferable to wait in a "safe" retreat rather than risk predation. In some spider species, mean body weight may increase enormously and rapidly when food is available (Miyashita 1991). Although *Neriene radiata* Walckenaer 1842 (referred to as *Linyphia marginata* in reference) do not emigrate when there is a shortage of food, they grow faster when food is available (Wise 1975). Under these circumstances, it may be preferable to wait on the likelihood of better conditions later.

Nephila, an orb web spider, moved significantly less in a rich environment, than in a poor environment (Vollrath 1985). Apparently *Nephila* produces an orb web that is more expensive than other orb webs (Vollrath & Houston 1986) and therefore they are less likely to relocate. The sub-social eresid, *S. lineatus* Latreille 1817, decreased web size and some stopped web building when food was supplemented (Pasquet et al. 1999). They suggest that the proximate cue for web relocation is the presence or absence of prey, rather than body condition. While food supplementation in mantids and cursorial spiders resulted in lower dispersal (Moran & Hurd 1997), favorable food conditions have been reported to increase dispersal in other spiders (Ward & Lubin 1993).

Dispersal of better-fed spiders was also

found in an orb web spider and the increased emigration was explained as risk-sensitive foraging (Gillespie & Caraco 1987). If the availability of food is important in the proximate decision to move, and if spiders are acting in a risk-sensitive manner, we predicted that they would move when the mean amount of food available per spider was less than their mean long-term requirements. They should remain at their present nest site if the prey available is more than their mean requirements. However, more spiders that obtained sufficient food showed a propensity to move. Although spiders in the unfed colonies obtained less food than their mean energy requirements, lost weight and many died, they showed little propensity to leave. They showed a preference to sit it out rather than risk moving, i.e., risk-averse behavior. Avilés & Tufino (1998) suggest that the costs of dispersal are so high that colonies of social spiders reach beyond optimal size and crash, rather than disperse.

Social spiders invest a large amount of silk in the production of closely woven retreats and in many sheets of capture web. Nests of *S. mimosarum* consist of a central retreat with numerous tunnels opening onto the lower surface, and a capture web of cribellate silk, which radiates out from this retreat. Under normal circumstances, in a social spider colony with its complex retreat and capture web, a number of spiders share these costs, so that the cost per spider is usually reduced. Silk is extremely expensive to produce and cribellate silk is more costly than sticky orb web silk (Tanaka 1989; Opell 1998). Non-adhesive webs are known to be costly to produce compared to sticky orb webs (Opell 1998; Tanaka 1989), and the webs of spiders that resorb silk (Opell 1998). Further, there is the cost of building a retreat. Studies on *S. lineatus*, a subsocial eresid, indicate that they lost 8% of their body mass and spent about six hours rebuilding webs (Pasquet et al. 1999). Spiders with more costly webs do not relocate often (Tanaka 1989). Emigrating social spiders may only have sufficient resources to relocate and build an energetically expensive nest under conditions of high prey availability. The spiders in our unfed colonies, without adequate food resources may remain in a site with little prey because they do not have the reserves required for relocating and rebuilding.

We know that *S. dumicola* may have a sol-

itary or social lifestyle (Henschel 1991), and single *S. mimosarum* do occur (Crouch et al. 1998). Individual spiders are therefore capable of initiating a new nest. However, the cost of setting up a new nest may be too high for spiders that are living at a low rate of food intake, and only well fed spiders may have the resources required to relocate. Well nourished individuals would therefore drive medium to longer distance dispersal.

High concentrations of food are thought to have resulted in gregarious behavior and an abundant food supply has been considered a major prerequisite influencing colony formation and the evolution of sociality (Rypstra 1986). However, in our experiment spiders did not reverse their sociality in response to starvation. We conclude that some factor other than mean amount of food available is more likely to trigger dispersal in these spiders. When food is abundant, they increase mass, and may emigrate if other factors (time of year, environmental conditions, spider size) are appropriate. In a previous experiment, significantly more spiders left during spring and when spiders were larger (Bodasing et al. 2001). However, when food is scarce, they stay to try to survive short-term changes. It would be less costly to remain especially if the retreat is intact and can provide some shelter, protection and prey.

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A COMPARISON OF THE DIVERSITY AND COMPOSITION OF GROUND-ACTIVE SPIDERS IN MKOMAZI GAME RESERVE, TANZANIA AND ETOSHA NATIONAL PARK, NAMIBIA

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ABSTRACT. Pitfall traps were used to census ground-active spiders in 12 different habitat types in protected savanna biomes in Tanzania and Namibia. With roughly equivalent trapping effort in the two areas, a total of 229 spider species and 40 families were trapped in Mkomazi Game Reserve and 151 species and 34 families in Etosha National Park. The family composition of the fauna of the two areas was similar, with Salticidae accounting for 17% (Mkomazi) and 14% (Etosha) of all species and Gnaphosidae accounting for 16% (Mkomazi) and 14% (Etosha) of the total. Other families that accounted for a significant proportion of species included Lycosidae (6–7%) and Zodariidae (6–7.5%). Despite the intensive trapping effort, there was no indication from species accumulation curves that a complete estimate of the spider species richness had been obtained from either area. The possible reasons for the differences in spider species richness and family composition in the two areas are discussed.

Keywords: Spider biodiversity, family composition, Etosha National Park, Mkomazi Game Reserve.

Although much is known about invertebrate diversity in temperate habitats, studies on species diversity in tropical ecosystems are more recent. A majority of studies have focused on tropical rainforest canopies because invertebrate diversity in them is so high. Very much less attention has been paid to invertebrate diversity in savanna areas, despite the fact that, broadly defined, savannas occupy more than twice the total land area of rain forests. This applies equally to research on spider diversity in tropical areas where the majority of reported work has been on forests (reviewed by Russell-Smith & Stork 1994).

In Africa, most inventories of savanna spiders have either been undertaken for purposes other than biodiversity assessment (e.g. Blandin & Celerier 1981; Russell-Smith 1981) or have been conducted over a limited time span or in a limited area (Russell-Smith et al. 1987; Lotz et al. 1991). There have been few attempts to census spider diversity over the full range of savanna habitats within a given area.

In this paper, assessments of spider biodiversity conducted as part of much larger surveys of invertebrate diversity in Mkomazi Game Reserve, Tanzania and Etosha National Park, Namibia are described. Both surveys censused spiders of the ground layer, field layer and tree canopies in the two sites but, for

logistical reasons, most effort was focused on the ground layer fauna. Pitfall trapping in 16 habitats ranging from dry grasslands to woodland or dry forest in both areas was used to assess spider diversity over a three year period. Trapping effort was very similar in both areas and the results are thus directly comparable.

METHODS

Study areas.—Mkomazi Game Reserve in northern Tanzania lies at approximately 4° S and between 38° and 39° E, adjacent to the Kenya border and forming a southern extension of the much larger Tsavo (West) National Park in Kenya. The park covers an area of about 3600 km² and varies in elevation from 630–1600 m. It is bounded to the South by the Usambara Mountains, to the West by the East Pare Mountains and to the East by the Indian Ocean. Apart from isolated hills rising to 1600 m elevation, the land surface is a gently inclined peniplane falling gradually from ca 1000 m in the West to ca 700 m in the East. Rainfall ranges from 800 mm in the West of the reserve to 200 mm in the East and most of the rain falls in two periods, in March and April and October to December.

The vegetation of the reserve consists of a mosaic of woodland, bushland, wooded or

bushed grassland and open grassland in which the boundaries between different vegetation types are often gradual and indistinct. Many of the wooded or bushy habitats are dominated by species of *Acacia* and *Commiphora*, either individually or as mixed stands and it is estimated that these may comprise some 70% of the total area of the reserve. Forest habitats are confined to isolated hilltops (principally in the West of the reserve), where dry montane forests are dominated by *Spirostachys africana* and *Brachylaena huillensis* and to a fringe of riverine forest along the Umba River in the East, dominated by leguminous trees of the genera *Afzelia*, *Albizia*, *Newtonia* and *Tamarindus*. Pure grassland is almost confined to low lying areas (locally known as "vleis") on black cracking clay soils which are subject to seasonal inundation. Grasslands vary in height from 25 cm or less in the dry season to almost 200 cm in perennial grasslands in the wet seasons.

Pitfall sampling was carried out in 12 distinct vegetation types as follows: Seasonally inundated grassland with *Acacia drepanolobium* on black cracking clay (vlei grassland), near Ndea Hill; Seasonally inundated grassland with *Acacia zanzibarica*, near Ngurunga; Grassland derived from montane *Spirostachys* forest, summit of Ibaya hill; Unburnt mixed grassland on foot slope, near Ibaya Camp; Unburnt *Acacia/Commiphora* woodland on lower hill-slope, near Ibaya Camp; Open *Acacia senegal* woodland, near Ndea Hill; Mixed riverine scrub, margins of Umba River; Mixed *Combretum* scrub, margins of Umba River; Mixed *Combretum* bushland, near Dindira dam; *Acacia senegal/A. nilotica* woodland, near Ubani; Dense *Dichrostachys cinerea* scrub, near Dindira dam; Montane *Spirostachys* forest, summit of Ibaya hill. These are listed in approximate order from habitats with the least tree cover to those with the greatest. Further details of these habitats can be found in Coe et al., 1998.

Etosha National Park is situated in the north of Namibia and lies along latitude 19° South between approximately 14° and 16° East longitudes. The park covers an area of 22,000 km² and is centred on Etosha pan, a very large area of seasonally flooded saltpan. The general land surface is extremely flat with isolated inselbergs to the south of the pan but with slightly larger hills in the extreme south and

west of the reserve. Rainfall ranges from about 450 mm in the East of the reserve to about 300 mm in the West. Nearly all rainfall falls between November and April but is extremely erratic, with some years with less than 30 mm total rainfall.

The range of vegetation types within the reserve is, in many respects, similar to that in Mkomazi Game Reserve, with woodland, bush and grassland habitats which intergrade gradually with one another. Differences in the vegetation of the two reserves include the absence of true forest habitats from Etosha and the much greater area of grassland or bushed grassland habitats here than in Mkomazi. In general, closed woodland is confined to the higher rainfall area of the east of Etosha and open grassland habitats become more frequent towards the West. Open grassland is however, found throughout the reserve both on saline soils and on shallow soils on calcrete. Another difference is that *Commiphora* species are much less abundant in woodland and bushland in Etosha than in Mkomazi and *Acacia* species, although widespread and common, rarely dominate woodland and bush in Etosha. Further details of the vegetation of Etosha can be found in Le Roux et al., 1988.

Pitfall trapping was conducted in the following 12 vegetation types: *Terminalia/Combretum* woodland, Beisebvlakte and Oshivelo; *Terminalia/Spirostachys* woodland, Leeu-drink; Mixed woodland, southeast corner of reserve; Open *Combretum/Kirkia* woodland on dolomite inselberg, Helio Hill; Dense shrub mopane bushland on calcrete, Natukan-aoka and Otjivalunda; *Colophospermum/Combretum* bushland, Ombika and Ongava; Open shrub mopane bushland on loam, Bitterwater; Open *Colophospermum/Combretum* bushland ("Kaokoveld"), Oliphantsrus; Mixed shrub/low tree savanna, near rain gauge 17; Mixed *Acacia/Terminalia* shrub bushland, Duineveld; *Eragrostis/Ennapogon* grassland ("sweet grassveld") on calcrete, Okaukuejo; *Sporobolus/Odysea* grassland, Andoni South and Andoni North. These are listed in approximate order from habitats with the greatest tree cover to those with the least. Further details of these habitats can be found in Le Roux et al. (1988).

Sampling Method.—In Mkomazi, diversity of ground-living spiders was studied with pitfall traps constructed from plastic coffee

beakers each 7 cm in diameter and 10 cm deep. Traps were spaced at a minimum of 2 m apart and filled to a quarter of their depth with water to which a trace of household detergent was added. To reduce disturbance resulting from daily emptying, two plastic cups were placed one inside the other and only the inside cup was removed from the ground. Trap contents were removed onto a 1 mm mesh sieve and preserved in 70% ethanol for subsequent sorting and identification. Normally, traps were placed in three rows of 10 traps spaced 5 m apart, and left in the field for periods of either three or six days before emptying. The contents of the 10 traps from each row were pooled at each site sampled. Sampling was most intensive at the two sites close to Ibya camp where pitfall traps were operated over six day periods in November 1994 and for six days in each month from April to August 1995. Samples from the remaining site were taken either over three days (vlei grassland near Ndea, grassland derived from montane forest on Ibya Hill and open *Acacia senegal* woodland near Ndea) or six days (all remaining sites other than the last one) in April 1995 or January 1996. Samples were taken over three days in April 1995 and six days in January 1996 in the montane forest (site 12). Total trapping effort in Mkomazi was 7,200 trap days.

A similar system was used in Etosha except that traps were 10 cm in diameter and 9 cm deep. A killing fluid of ethylene glycol diluted to 50% with water was used. Here, traps were placed in four rows of 10 and were emptied after four days in the field. The catch from each row of traps was pooled. Sampling was carried out at the first 6 sites listed above in November 1996 and January, March, June and November 1997. Sampling from the second six sites listed was in March 1998 only. The total trapping effort at this site was 7,680 trap days. Voucher specimens of the Salticidae from Mkomazi Game Reserve are deposited in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium while those for all other families remain in the author's collection. Voucher specimens of all spiders from Etosha National Park are deposited in the National Museum of Namibia, Windhoek.

RESULTS

Family and species richness and diversity.—The family composition of the spider

fauna for the two study areas is shown in Table 1. In both areas, Salticidae and Gnaphosidae accounted for the largest proportion of spider species, each representing approximately 16%–17% of all species at Etosha and 14% of all species at Mkomazi. Other families that were well represented in both areas included Lycosidae (~ 6%–7% of all species) and Zodiidae (~ 6%–7.5% of all species). Corinnidae, Theridiidae and Thomisidae were well represented in traps at Mkomazi but were rare in traps in Etosha. Prodidomidae represented 9% of all species at Etosha but less than 2% in Mkomazi. The families Amaurobiidae, Clubionidae, Ctenidae, Hahniidae, Mimetidae, Miturgidae, Mysmenidae, Telemidae, Tetrablemmidae, Tetragnathidae, Theridiosomatidae and Uloboridae, 22 species altogether, were only recorded in traps at Mkomazi. Conversely, the families Ammoxenidae and Siciidae, 7 species altogether, were only recorded from traps at Etosha. There were 78 more spider species and 6 more families recorded from Mkomazi Game Reserve than from Etosha National Park (Table 1).

Efficiency of trapping.—The conclusions drawn as to the differences in spider species richness between the two areas will depend to some extent on how complete the sampling effort was in each. The cumulative numbers of spiders trapped is plotted against the cumulative number of trap days for both sites in Fig. 1. While the rate of accumulation of new species trapped was always greater in Mkomazi than in Etosha, it is evident that in neither area does the curve for species accumulation over sampling effort approach an asymptote. However, the rate of species accumulation does appear noticeably lower in Etosha than in Mkomazi from 5,000 trap days to 7,600 trap days.

DISCUSSION

Despite the relatively intensive sampling effort in both of the study areas, it is evident from Fig. 1 that the census of species was far from complete. Although this may, in theory, mean that the difference between the two sites in spider species richness is less than suggested in this study, there is little reason to suppose that species richness would actually be higher at Etosha than at Mkomazi.

The family composition of the ground-active spider faunas in both areas studied is fair-

Table 1. The family and species composition of spiders from pitfall traps in Etosha National Park, Namibia and Mkomazi Game Reserve, Tanzania.

Etosha National Park, Namibia		Mkomazi Game Reserve, Tanzania	
Family	Species	Family	Species
Agelenidae	3	Agelenidae	1
Ammoxenidae	6	Amaurobiidae	3
Araneidae	0	Araneidae	6
Atypidae	1	Atypidae	1
Barychelidae	1	Barychelidae	2
Caponiidae	1	Caponiidae	2
Corinnidae	1	Clubionidae	1
Cyrtacheniidae	9	Corinnidae	10
Dictynidae	1	Ctenidae	4
Dipluridae	1	Cyrtacheniidae	4
Gnaphosidae	24	Dictynidae	1
Hersiliidae	1	Dipluridae	1
Heteropodidae	1	Gnaphosidae	32
Idiopidae	4	Hahniidae	1
Linyphiidae	3	Hersiliidae	1
Lycosidae	11	Heteropodidae	3
Nemesiidae	2	Idiopidae	7
Ochyroceratidae	1	Linyphiidae	8
Oonopidae	4	Lycosidae	13
Oxyopidae	3	Mimetidae	1
Palpimanidae	5	Miturgidae	5
Philodromidae	5	Mysmenidae	1
Pholcidae	4	Nemesiidae	1
Prodidomidae	14	Ochyroceratidae	1
Salticidae	26	Oonopidae	8
Scytodidae	1	Oxyopidae	9
Segestriidae	1	Palpimanidae	4
Selenopidae	1	Philodromidae	6
Sicariidae	1	Pholcidae	3
Theraphosidae	1	Prodidomidae	4
Theridiidae	1	Salticidae	31
Thomisidae	3	Segestriidae	2
Zodariidae	9	Telemidae	2
Unidentified	1	Tetrablemmidae	1
		Tetragnathidae	1
		Theridiidae	14
		Theridiosomatidae	1
		Thomisidae	15
		Uloboridae	1
		Zodariidae	17
Total species	151	Total species	229
Total families	34	Total families	40

ly typical of those found in earlier studies of semi-arid savannas elsewhere in Africa (Russell-Smith 1981, Russell-Smith et al. 1987, Lotz et al. 1991). In all of these areas, gnaphosids and salticids are among the most diverse families, with the former apparently dominating drier sites and the latter more spe-

cies rich in somewhat higher rainfall areas. In the very humid savanna at Lamto, Côte d'Ivoire (mean annual rainfall 1300 mm), salticids accounted for 19% of all species and gnaphosids for only 6.7% (Blandin & Celerier 1981). Other species rich families in previously studied sites include Zodariidae (4.8–

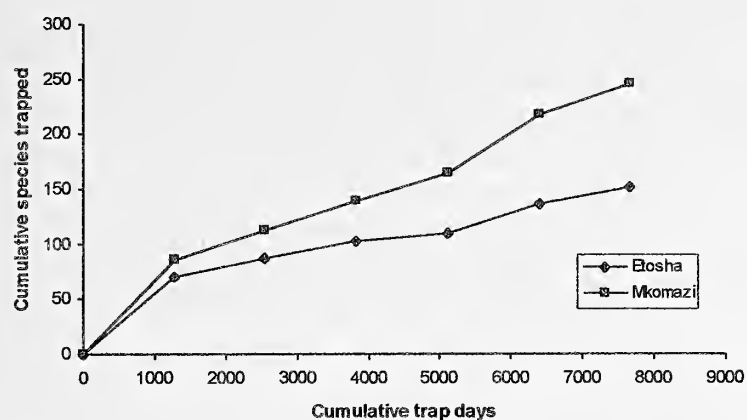


Figure 1.—Cumulative numbers of spider species trapped in Mkomazi Game Reserve (Tanzania) and Etosha National Park (Namibia).

12.8% of all species) Lycosidae (8.5–21.5%), Oxyopidae (2.1–5.7%) and Thomisidae (3.3–17.0%). However, the results differ from those of Whitmore et al. (2002) who found that gnaphosids represented only a small proportion of the total spider fauna of a savanna area adjacent to Kruger National Park in South Africa. They suggest that this was probably a result of the very high level of disturbance of pitfall traps by baboons (Whitmore, pers. comm.).

If it is assumed that the difference in spider species richness between Mkomazi and Etosha is real rather than an artifact of under-sampling, what factors might account for the difference? There are at least three possible explanations, none of which are necessarily mutually exclusive: a) a latitudinal gradient in spider diversity exists, with highest diversity at the equator and decreasing diversity with increasing latitude; b) spider diversity is related to mean annual rainfall, with higher diversity in wetter areas; c) there are unique differences in the regional pools of available spider species in the two regions which determines the diversity in each area. There is some support for the concept of a latitudinal gradient of diversity of spiders, at least between the equator and the northern hemisphere. For example, Weselowska & Russell-Smith (2000) present empirical evidence for an area-specific decline in species richness of salticids between Mkomazi (4° S) and the UK (~ 55° N) of approximately one order of magnitude, although there are insufficient data sets from Africa to place very great reliance on this conclusion. However, Platnick (1991) has suggested that there is little decline in diversity of spiders between the equator and southern latitudes of the neotropical region, al-

though without supplying comparative data to support the contention.

Although the range of annual rainfall in the two areas studied overlaps (see site descriptions above), there is little doubt that Etosha National Park is, overall, considerably more arid than Mkomazi Game Reserve. Much of the former has annual rainfall of less than 400 mm and complete failure of annual rains is a regular, if infrequent occurrence. By contrast much of Mkomazi, including the areas in which most of the pitfall trapping was conducted, has annual rainfall above 550 mm, and here complete failure of both the short and long rains is extremely rare. Some support for the importance of rainfall in determining ground-active spider richness can be seen in the relative proportion of gnaphosoid species (Ammoxenidae, Gnaphosidae and Prodidomidae) in the two areas, 29% of the total in Etosha and 16% in Mkomazi. Evidence from studies of other savanna sites in Africa does suggest that gnaphosids are characteristically more diverse in more arid sites while the reverse applies to salticids.

A final possibility, that there is a large difference in the size of the regional pools of spider species from which the fauna of the two areas was drawn, is more difficult to establish. That there are differences in the occurrence of spider families represented in the two regions seems certain. Thus, Griffin (1998) does not include Tetrablemmidae, Telemidae, Cyatholipidae and Symphytognathidae in her list of spider families recorded from Namibia while all are recorded from Tanzania. Conversely, Ammoxenidae are well represented in Namibia but are known to be absent from East Africa. However, none of these families contributed many species to the total from either area studied and it is probably the size of the regional pools of species in the more diverse families, such as Salticidae and Gnaphosidae, that is more pertinent here. Unfortunately, the systematic data for any of the larger families of spiders in any region of Africa is currently woefully inadequate. As an example, among the 69 species of salticids recorded from Mkomazi Game Reserve, nearly half were found to be new to science (Weselowska & Russell-Smith 2000). Until the systematic understanding of the larger spider families in Africa is greatly improved, it is difficult to assess

how far the size of regional species pools affects spider diversity of specific areas.

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ON THE NATURE OF AGROBIONT SPIDERS

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ABSTRACT. Results from a 10 year survey of spiders in Hungarian arable and natural grassland habitats are cumulated in order to reveal the key characteristics of agrobiont species. We define agrobionts as species that reach high dominance in agroecosystems. The most dominant species, *Pardosa agrestis*, on average accounted for 40% of the total spider population in Hungarian arable fields. The presence of agrobionts led to a strong skew in arable spider community species distribution. Regardless of the over-dominance by agrobionts, arable spider communities had a potential for very high species richness. The agrobiont segment of arable spider communities showed very little field-to-field or regional variation, i.e. the same agrobiont species occurred in all fields. Agrobionts were indicators of arable habitats, and were rare in other habitat types, but in many species preferences for specific natural habitat types could be shown. These natural habitat types were often strongly abiotically driven, frequently disturbed habitats. The life cycle of agrobionts showed synchronization with the arable crop-growing season. While many closely related non-agrobiont species had maturity and reproductive periods either earlier or later than the main crop vegetation period, agrobionts invariably reached adulthood and reproduced during that period. Association with frequently disturbed natural habitats and phenological synchronization with the annual arable disturbance regime are such traits that support the theory that agrobiont species are adapted to predictably ephemeral habitats.

Keywords: Community structure, arable fields, cyclic colonization, life history strategy

Agricultural habitats are artificially created and maintained by periodic disturbances to be more uniform than most natural habitats. Agricultural systems have been present for only a short evolutionary time period. Thus they are likely to lack co-evolved animal communities. Many ‘empty niches’ may offer themselves for colonization both by herbivorous and predatory animals from natural habitats. It is still debated as to what degree these habitats are recolonized repeatedly, or to what extent they are self-perpetuating systems, at least at the metapopulation level (Duffey 1978; Bishop & Riechert 1990; Wissinger 1997). To study the community assembly rules in agricultural areas, and to study the ecological characteristics of the individual species should be revealing for the basic ecological phenomena, and may provide opportunities to shift the balance in agricultural communities towards beneficial organisms, and thus promote biological control.

Considering communities of predatory arthropods in agricultural areas, and those of spiders in particular, it has been observed that

a few super-abundant species often dominate these systems. The dominating species, since the seminal paper by Luczak (1979) are called ‘agrobiont’ species. The dominance of agrobionts has been established in various crops and geographical areas (Richman et al. 1990; Nyffeler & Breene 1992; Blick et al. 2000) but many questions about the ecological strategies of agrobionts are still open. Duffey (1978) and Luczak (1979) predicted that agrobionts are habitat generalists, “eurytopic” species, that occur sometimes in quite contrasting habitats. Recently Wissinger (1997) proposed that agrobionts are species with an “adaptation to predictably ephemeral habitats” (APEH). According to the APEH hypothesis agrobionts are not generalist species, rather they evolved a specific strategy, called the “cyclic colonization” strategy. Through cyclic colonization, agrobionts can escape the regularly occurring disturbances by dispersing to permanent refugia. The strategy requires specific life history adaptations, with special regard to synchronization with the periodic disturbances through the timing of reproduc-

Table 1.—Sampling locations that provided data for the meta-analysis. (A = alfalfa, C = cereal, G = grassland (No. of sub-types), P = pitfall, D = suction sampling.)

County	Settlement	No. of sites	Habitats	Method
Baranya	Nagyharsány	1	G(2)	P
Csongrád	Királyhegyes	2	A, G(2)	P, D
Heves	Hatvan	1	C	P
Heves	Recsk	1	G(1)	D
Nógrád	Bánk	1	C	D
Nógrád	Diósjenő	1	A	D
Nógrád	Pásztó	1	C	D
Nógrád	Rétság	1	C, G(1)	D
Nógrád	Romhány	1	A, G(1)	D
Pest	Kartal	2	C	P
Pest	Nagykovácsi	3	A, C, G(2)	P, D
Pest	Páty	3	A, C, G(1)	D
Pest	Budapest	1	G(1)	P, D
Tolna	Decs	1	A, C	D
Tolna	Felsőnána	5	A, C	P, D
Tolna	Szekszárd	1	A, C	D
Tolna	Tevel	1	A, C	P, D
Vas	Szombathely	2	C	P
Veszprém	Somlóvásárhely	1	G(1)	P

tion, and the presence of various colonizer and overwintering stages. Other ecological characteristics, such as competitive ability (Marshall & Rypstra 1999), tendency for cannibalism and intraguild predation (Wagner & Wise 1996; Hodge 1999; Samu et al. 1999b), and colonization power (Richter 1970; Sunderland & Topping 1993; Marshall et al. 2000) are additional features that might be important characteristics of the agrobionts' ecological persona. Although the importance of life history characteristics has been stressed in earlier studies (Duffey 1978; Toft 1989), no comprehensive comparisons of regional agricultural spider faunas and those occurring in natural habitats has been made, to date.

The present paper tries to reveal the ecological nature of the agrobiont species in Hungarian arable fields. We hope to find common ecological features of agrobiont species, and in this way get closer to their secret of being successful in human influenced habitats. Agrobionts are characterized through a meta-analysis of 10 years of survey data on spider assemblages of Hungarian arable fields. In the meta-analysis we seek to clarify (i) which are the main agrobionts in Hungarian arable fields; (ii) how the presence of these superdominant species affects the diversity and

dominance structure of the whole spider community, as compared to natural grassland communities; (iii) how agrobiont compositions vary field-by-field and regionally; (iv) what the original natural habitats of the agrobionts are; and (v) what commonalties can be found in their life cycles, and how do these relate to the disturbance regime of arable fields?

METHODS

Arachnological results from various faunistic and agro-ecological projects on arable fields (Samu et al. 1996; Tóth & Kiss 1999; Szinetár & Miltényi 2000; Samu et al. 2001) were accumulated into a common database (Samu 2000). The present paper provides a meta-analysis of these data, focused on the ecology of agrobiont species.

The sampling methods were pitfall trapping and hand-held suction sampling. Original survey datasets contained information on c. 110,000 individuals, but we restricted the scope of the analysis by the following criteria: (i) only adults were considered; (ii) only those data sets were included in which sampling lasted for at least one year for the given field/habitat patch and for the given method, and (iii) the total catch of spiders was greater than

Table 2.—The 16 most dominant arable (cereal and alfalfa) spider species. Last two columns indicate the percentage of fields a species was present out of all the fields sampled by the respective method.

Species	Family	Total catch	Dominance (%)	In suction sampled fields (%)	In pitfall sampled fields (%)
<i>Pardosa agrestis</i> (Westring 1861)	Lycosidae	10,423	38.96	88.46	100.00
<i>Meioneta rurestris</i> (C. L. Koch 1836)	Linyphiidae	3,886	14.53	100.00	58.82
<i>Oedothorax apicatus</i> (Blackwall 1850)	Linyphiidae	3,602	13.46	65.38	82.35
<i>Pachygnatha degeeri</i> Sundevall 1830	Tetragnathidae	1,683	6.29	80.77	94.12
<i>Erigone dentipalpis</i> (Wider 1834)	Linyphiidae	1,239	4.63	80.77	47.06
<i>Tibellus oblongus</i> (Walckenaer 1802)	Philodromidae	546	2.04	92.31	35.29
<i>Drassyllus pusillus</i> (C. L. Koch 1833)	Gnaphosidae	346	1.29	15.38	88.24
<i>Xysticus kochi</i> Thorell 1872	Thomisidae	322	1.20	46.15	76.47
<i>Pisaura mirabilis</i> (Clerck 1757)	Pisauridae	279	1.04	65.38	23.53
<i>Robertus arundineti</i> (O.P.-Cambridge 1871)	Theridiidae	268	1.00	26.92	58.82
<i>Araeoncus humilis</i> (Blackwall 1841)	Linyphiidae	226	0.84	73.08	47.06
<i>Trichoncoides piscator</i> (Simon 1884)	Linyphiidae	216	0.81	15.38	29.41
<i>Mangora acalypha</i> (Walckenaer 1802)	Araneidae	202	0.76	61.54	11.76
<i>Zelotes mundus</i> (Kulczynski 1897)	Gnaphosidae	172	0.64	0	29.41
<i>Meioneta simplicitaris</i> (Simon 1884)	Linyphiidae	166	0.62	73.08	29.41
<i>Lepthyphantes tenuis</i> (Blackwall 1852)	Linyphiidae	148	0.55	38.46	41.18
other species	207 species	3,028	11.32		
Total		26,752			

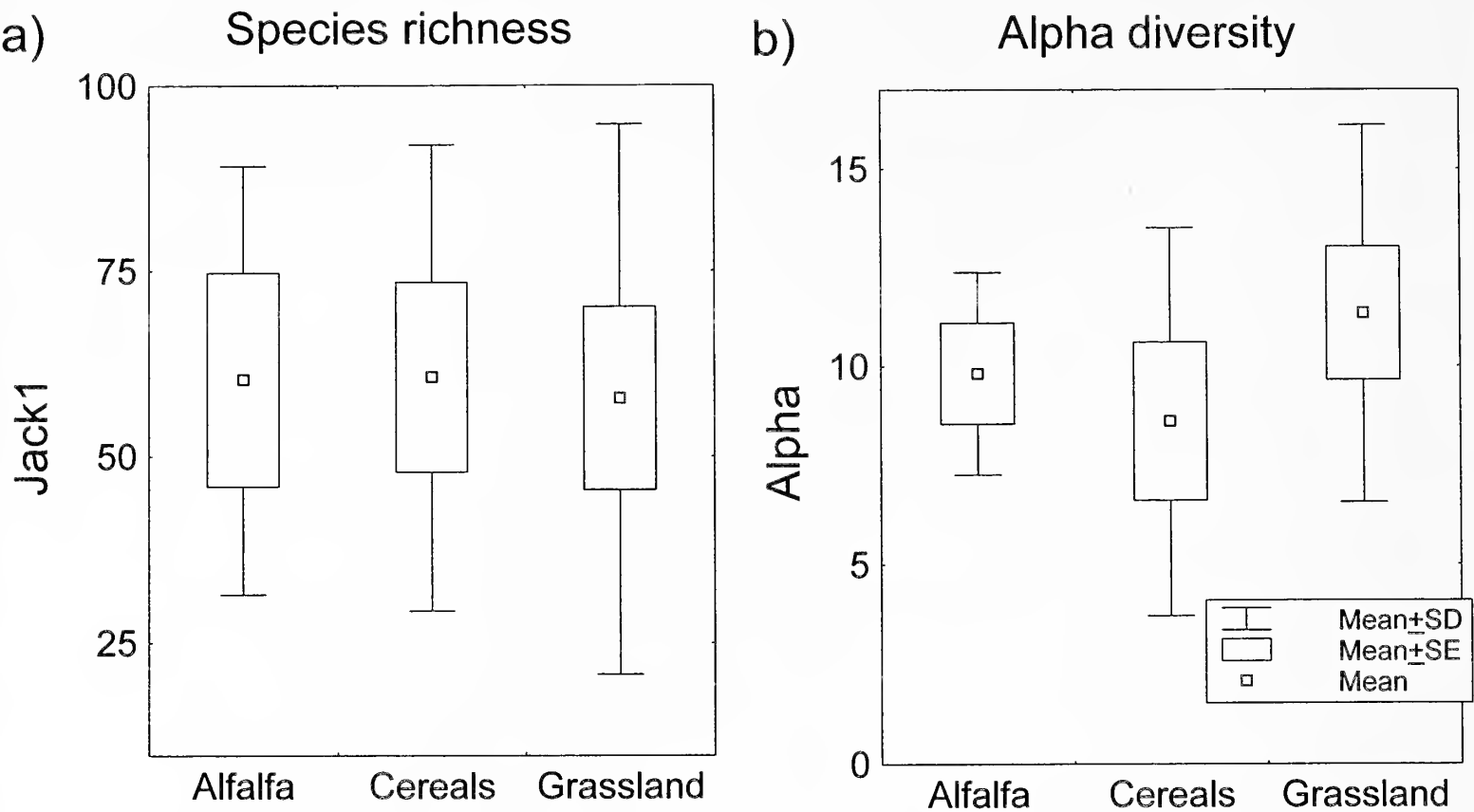


Figure 1.—a. Species richness (estimated by first order Jacknife estimator) and b. alpha diversity of spider communities of habitat patches/fields belonging to the main habitat types investigated.

100 adult individuals for the field; (iv) results were included from samples taken between 1990 and 2000. Since species composition is dependent on trapping method, and pitfall trapping yielded many more adults, community structure and field-by-field comparisons were made relying on pitfall trap data only.

The spatial unit of the analysis was a field

(fields were typically 30 ha, ranging between 1.5 & 250 ha), or the natural equivalent, a “habitat patch”. Samples conforming to the above criteria were taken in 47 field/habitat patches at 30 sites. The sites were in 19 localities in eight counties in Hungary (Table 1). The main sampled habitat types were cereal fields, alfalfa fields and natural or semi-natural grassland areas. Grasslands could be classified into five different sub-types: secondary, mesophile, saline, rock grasslands, and moist meadows. Secondary grasslands developed mainly on sites previously occupied by agricultural fields or intensive pastures, later abandoned but might receive occasional disturbances. They are colonized by numerous pioneering, introduced or ruderal species, but a natural regeneration has already started. The disturbance-induced simplified stratification is typical for the structure. Mesophile grasslands are a category for dense perennial grasslands of lowlands and hills, fertilized and well-drained. They are species rich grasslands with a complex structure. Light disturbance, such as occasional grazing or using them as hay meadows is possible. Saline grasslands are comprised of salt steppes and saltmarsh meadows (and all the continuum between them) of the Pannonic plain. Large expanses of salt steppe form an open landscape of short-grass

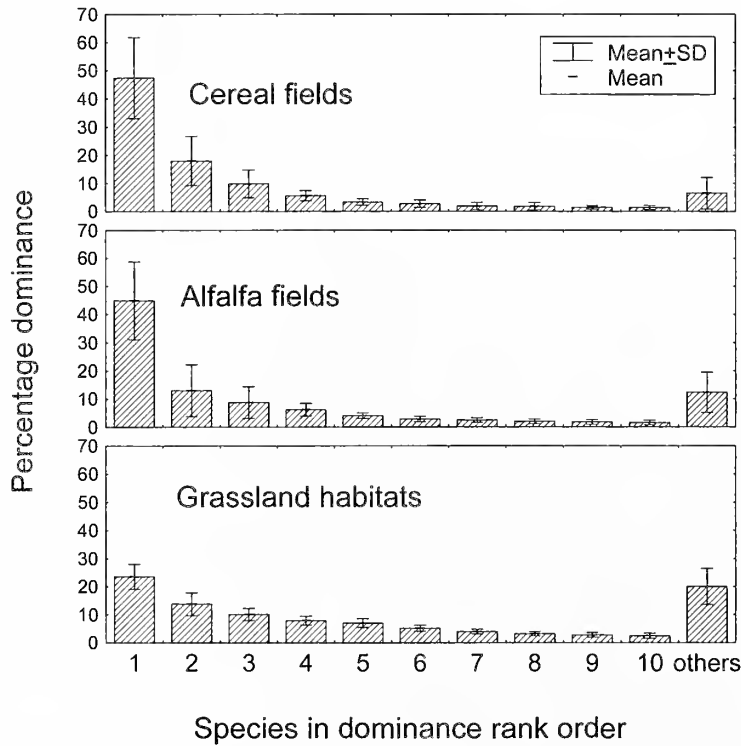


Figure 2.—The dominance structure of spider communities of habitat patches/fields belonging to the main habitat types investigated.

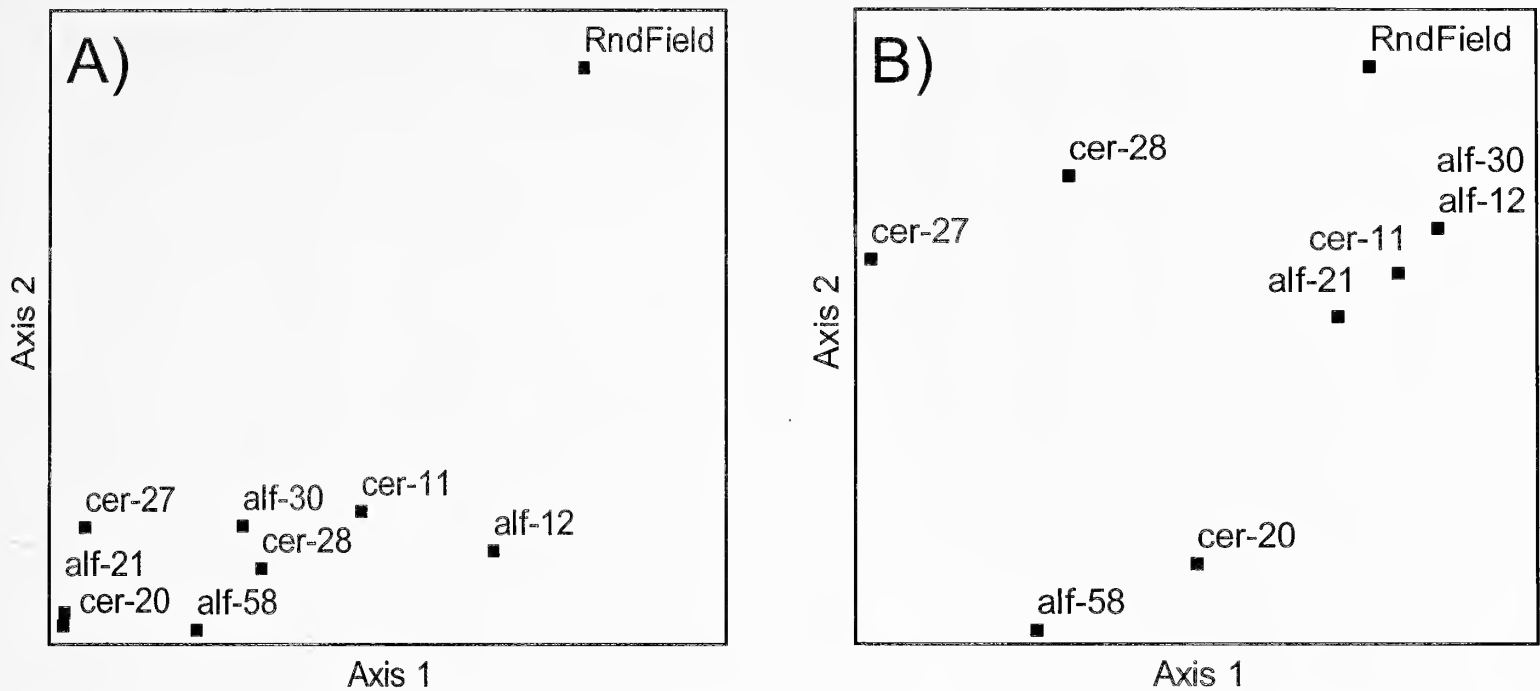


Figure 3.—Non-Metric Scaling (NMS) ordination plots, representing the Soerensen similarity structure of selected arable fields, when A) the first eight dominant species; and B) the second eight dominant species are considered. The random field was generated by shuffling mean dominances of the first 16 dominant species. (alf-x denotes alfalfa field; cer-x stands for cereal field, where x is identifier number of the given field; RndField denotes the hypothetical field where spider community was created by randomization [see text for details].)

swards on slightly elevated ground and of rills, eroded shallow depressions with bare or sparsely vegetated saline soils. Because of poor drainage, the rills experience yearly flooding in springtime, but dry out completely by summer. The structure is simple and open. Rock grasslands are xero-thermophile grasslands, on rocky areas or on rendzinas on hilly or montaneous areas. They occupy sites with a warmer, drier microclimate, in particular south-facing slopes with extreme conditions of insolation, temperature variation and evaporation. They are rich in plant species, but the structure is dominated by low grasses. Moist meadows develop on moderately to very nutrient-rich, alluvial or fertilized, wet or damp soils, often inundated at least in winter, and relatively lightly mowed or grazed. They include a large number of distinctive and often species-rich communities, many of which harbor specialized and rare species of plants.

RESULTS AND DISCUSSION

Agrobionts and agricultural spider communities.—Taken together all arable (cereal and alfalfa) data sets, a very distinctive list of the most dominant species arises (Table 2). The most dominant species are, by our definition, the agrobiont species. We regard any delimitation where a borderline between dom-

inant and non-dominant species should lie to be arbitrary, but considering a rather conservative 1% minimum dominance limit (i.e. an agrobiont species should be represented by more than 1% of all the individuals in the sampled assemblage) seems to be practical. It is also important to consider how widespread is the occurrence of a species in the considered crop(s). The rest of the analysis concentrates on the species listed in Table 2 and refers to species that occur on more than 75% of the fields and are above the 1% dominance threshold as “agrobionts”. Species that are below this limit, but still common in fields are called “agrophile” species after Luczak (1979).

Given the overwhelming dominance of agrobionts in arable fields, it is of interest to see how overall community structure is affected by them, what room is left for other species, and how agricultural spider community structure compares to the closest natural systems, grassland habitats. Species richness of cereal, alfalfa and grassland field/habitat patches was estimated from pitfall trap data with the first-order Jackknife richness estimator (Fig. 1a) using EstimateS (Colwell 1999), which gives a rather conservative estimate of species richness. Alpha diversity (Magurran 1988) for the same data set was

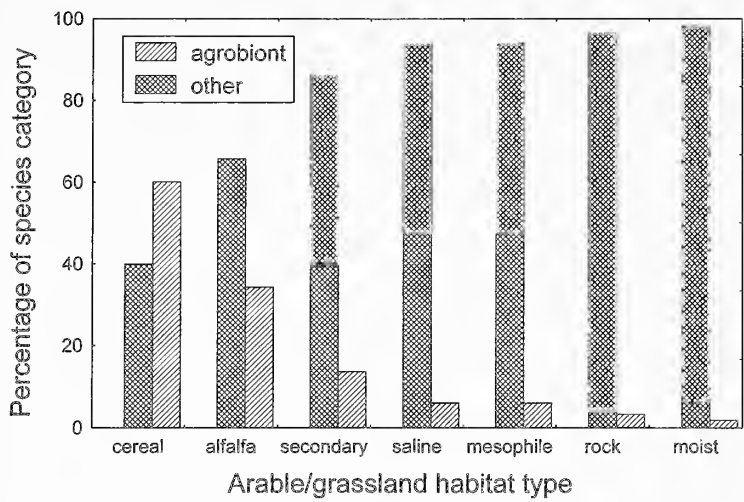


Figure 4.—Percentage representation of agrobiont spiders (first eight species in Table 2) in various habitat types in Hungary.

also calculated (Fig. 1b). Variation for both species richness and diversity values was high (mean $CV_{richness} = 54.0\%$, mean $CV_{diversity} = 43.3\%$, where CV = coefficient of variation), and no significant difference could be shown among the different habitat types in either measure (one way ANOVA, richness: $F = 0.015$, $df = 2, 15$, ns; diversity: $F = 0.649$, $df = 2, 15$, ns).

While agricultural spider communities were not different in terms of species richness and diversity from the natural grassland communities, the dominance structure of the agricultural and natural communities showed a marked difference (Fig. 2). The first most dominant species of each field/habitat patch had a significantly higher dominance value in the arable habitats than in the grassland habitats (one way ANOVA: $F = 10.031$, $df = 2, 19$, $P < 0.005$, Tukey HSD test at $P = 0.05$: cereal and alfalfa ns, grassland significantly different from both). The descent of the dominance curves also differed significantly between arable and grassland habitats, being less steeply descending in the later (ANCOVA on log transformed dominance, habitat type*rank interaction: $F = 12.477$, $df = 2, 214$, $P < 0.0001$).

The high species richness and diversity found in some of the studied agricultural fields contradicts the traditional view of the impoverishment of these habitats (Nyffeler et al. 1994). While arable fields clearly have the capacity for high diversity, maybe it is even more important to point out large between field variability. Toft (1989) reported that two cereal fields were as diverse in Denmark as the best natural habitats; in Poland only about

Table 3.—Indicator species analysis (resulting in the species and habitat specific Indicator Value), conducted according to the method by Dufrene and Legendre (1997). P values were obtained by Monte Carlo analysis, performed by PC-ORD (McCune & Mefford 1999).

Comparison	Indicated habitat (where Indicator Value is maximal)	No. of indicator species ($P < 0.05$)	No. of agrobionts in indicator species	First three species, which significantly indicate the habitat	
cereal-alfalfa	cereal	0	0		<i>Pardosa hortensis</i> , <i>Zelotes longipes</i>
	alfalfa	2	0		<i>Pardosa agrestis</i> , <i>Pachygnatha degeeri</i> , <i>Oedothorax apicatus</i>
cereal-grasslands	cereal	27	9		<i>Hogna radiata</i> , <i>Centromerus sylvaticus</i>
	grasslands	2	0		<i>Pardosa agrestis</i> , <i>Oedothorax apicatus</i> , <i>Pachygnatha degeeri</i>
alfalfa-grasslands	alfalfa	15	7		<i>Oxyptila atomaria</i>
	grasslands	1	0		<i>Pardosa agrestis</i> , <i>Pachygnatha degeeri</i> , <i>Oedothorax apicatus</i>
arable-grasslands	arable	26	8		<i>Centromerus sylvaticus</i> , <i>Hogna radiata</i> , <i>Oxyptila pullata</i>
	grasslands	7	0		

Table 4.—Habitat preferences of some agrobiont and agrophile spider species. Data obtained from Hänggi et al. (1995). (Abundance values were summed after giving values to abundance categories as follows: Rare = 1, Fairly common = 5, Common = 10 individuals.)

<i>Pardosa agrestis</i>			<i>Meioneta rurestris</i>			<i>Oedothorax apicatus</i>		
Habitat	Abund.		Habitat	Abund.		Habitat	Abund.	
Cereals	284		Cereals	264		Cereals	612	
Cultivated grassland	224		Soil after surface mining	205		Saline grassland	326	
Beet	100		Shrubs, hedges, cemeteries	165		Cultivated grassland	196	
Rye-grass/fertilized pastures	67		Brometalia	132		Beet	160	
Saline inland areas	60		Rye-grass/fertilized pastures	107		Coastal dunes	117	
Pioneer areas	52		Potatoes	83		Rye-grass/fertilized pastures	116	
<i>Erigone dentipalpis</i>			<i>Pachygnatha degeeri</i>			<i>Drassyllus pusillus</i>		
Habitat	Abund.		Habitat	Abund.		Habitat	Abund.	
Saline grassland	366		Cereals	467		Brometalia	71	
Cereals	310		Rye-grass/fertilized pastures	318		Dry, semi-dry grasslands	61	
Cultivated grassland	270		Moist meadows	241		Fers meadows	37	
Rye-grass/fertilized pastures	213		Cultivated grassland	177		Hedges	32	
Lawns in parks	176		Fers meadows	176		Forests edges	32	
Beet	160		Littoral areas, moist	145		Cultivated grassland	32	
<i>Xysticus kochi</i>			<i>Robertus arundineti</i>			<i>Araeoncus humilis</i>		
Habitat	Abund.		Habitat	Abund.		Habitat	Abund.	
Coastal dunes	202		Saline grassland	127		Cereals	120	
Brometalia	95		Raised bogs	37		Cultivated grassland	79	
Soil after surface mining	76		Dwarf shrub heath	36		Clover, alfalfa	40	
Dry, semi-dry grasslands	59		Beet	31		Rye-grass/fertilized pastures	32	
Cereals	58		Moist meadows	16		Saline inland areas	30	
Cultivated grassland	46		Cereals	16		Brometalia	26	

Lycosidae life cycles

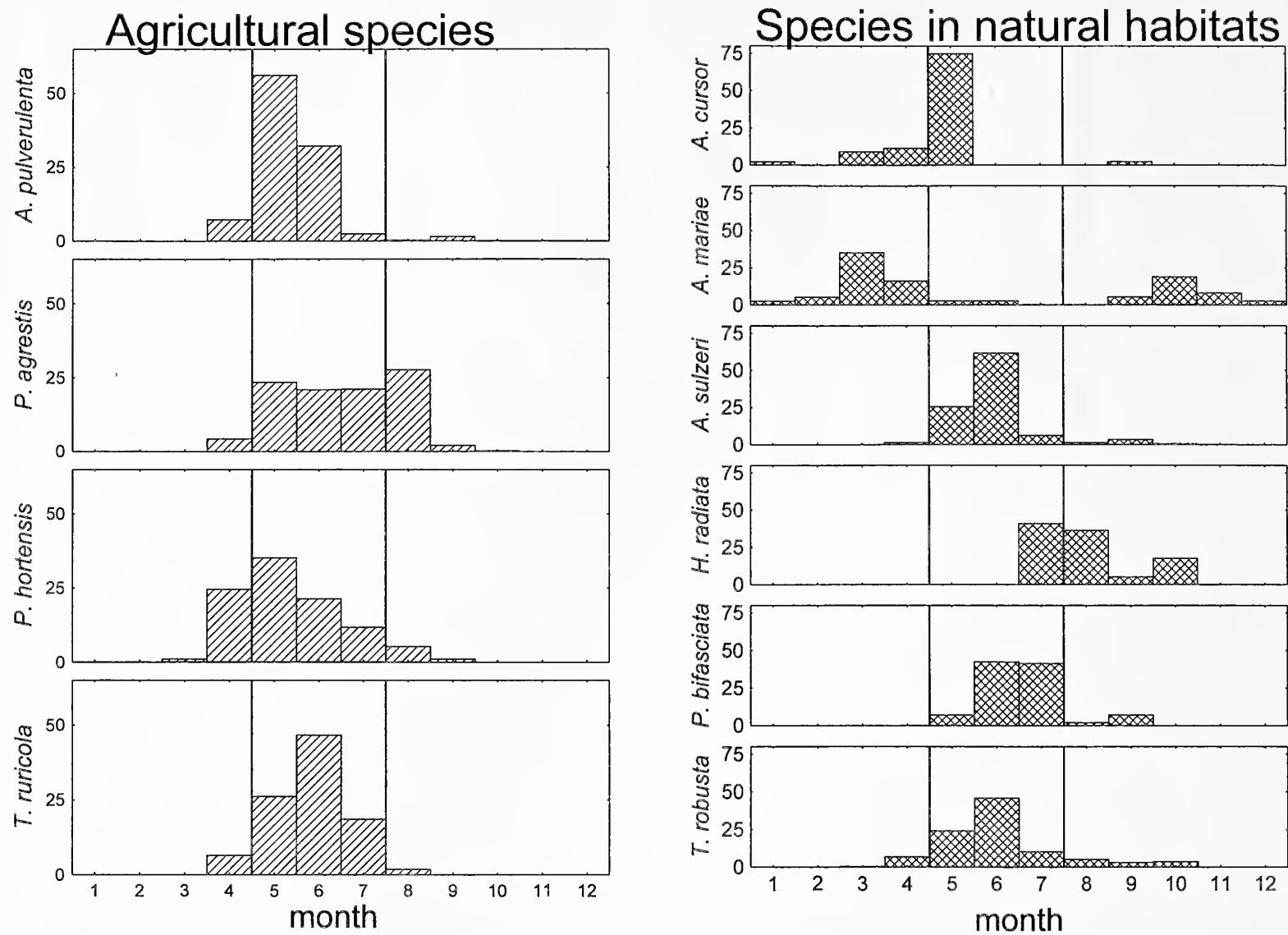


Figure 5.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Lycosidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Alopecosa pulverulenta*, *A. cursor*, *A. mariae*, *A. sulzeri*, *Pardosa hortensis*, *P. bifasciata*, *Hogna radiata*, *Trochosa robusta*, *T. ruricola*.

half of that richness was found (Luczak 1975). Both in the US (Richman et al. 1990) and Hungarian (Samu et al. 1996) alfalfa fields there were also high between field and regional differences in spider species richness. The establishment of the causes for this variation is an important task for both agricultural ecologists and conservationists. There is likely to be multiple causation, including structural diversity (Sunderland & Samu 2000), management intensity, pesticide use (Altieri 1994; Jenser et al. 1999), field size, and landscape structure (Nyffeler & Breene 1992; Samu et al. 1999a; Tóth & Kiss 1999).

Variation in agrobiont composition of arable fields.—Unlike species richness, very little variation was found in the agrobiont composition of the different arable fields sampled. The first 8 species were virtually ubiquitous, and dominance orders showed very similar

patterns. To study the magnitude of similarity, 8 fields with large enough sample sizes were selected (4 cereal, 4 alfalfa), and, relying on pitfall trap data, the spider community of the first 16 most dominant species was considered (Table 2). A ‘random field’ was also generated, in which the average dominance values of the first 16 species were shuffled. The fields were ordinated by non-metric scaling (NMS) (Clarke 1993), first by the first eight most dominant species, then by species of dominance rank 9–16. The ordination plots show (Fig. 3), that regarding the first 8 dominant species, fields were similar to each other (mean Soerensen similarity \pm SD = 0.61 ± 0.145), and dissimilar to the random field, while for species of dominance rank 9–16 similarity to each other was much lower (mean Soerensen similarity \pm SD = 0.35 ± 0.140), and they were not as distinctly sepa-

Linyphiidae life cycles

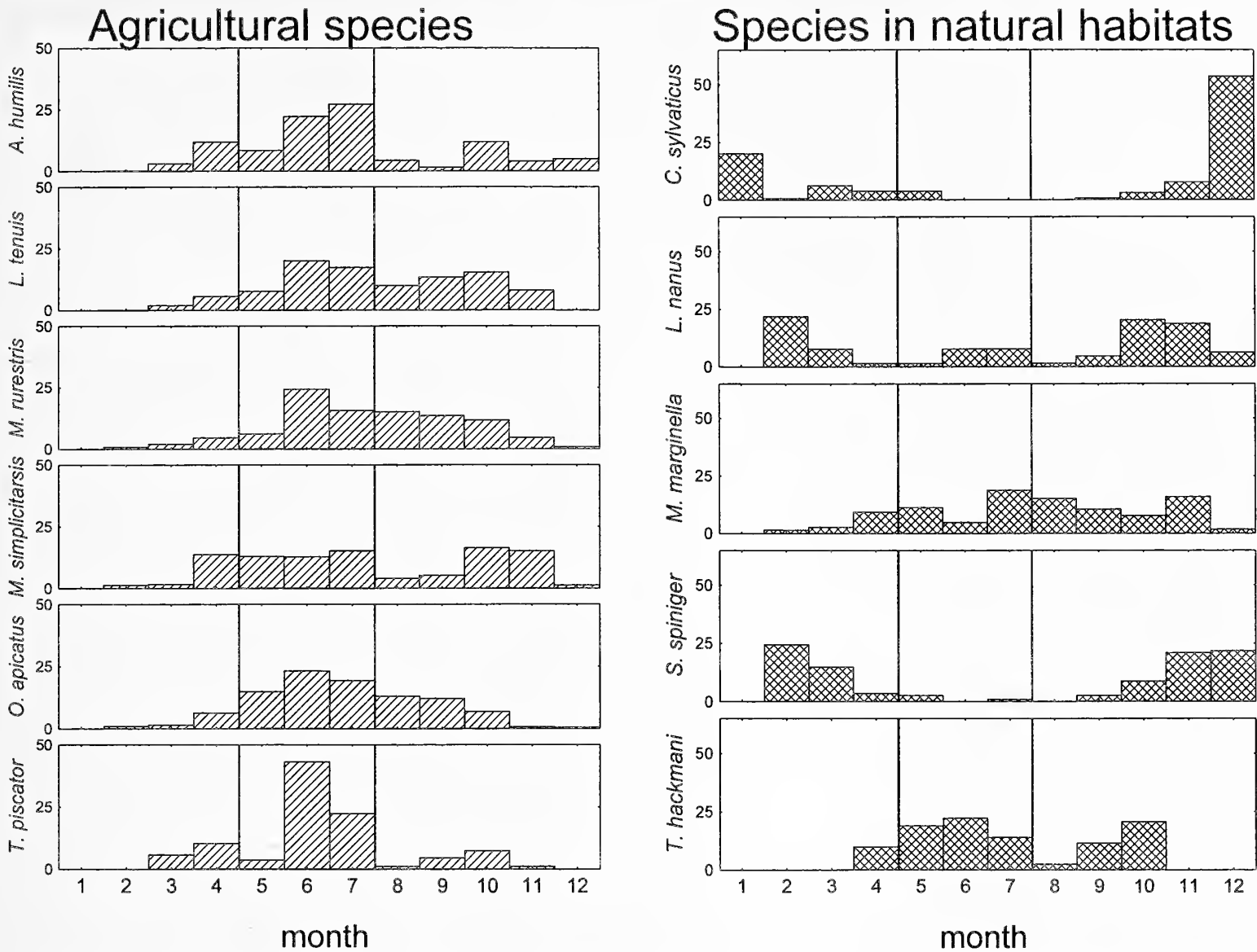


Figure 6.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Linyphiidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Centromerus sylvaticus*, *Leptyphantes nanus*, *Minicia marginella*, *Sintula spiniger*, *Trichoncus hackmani*.

rated from the random field (Fig. 3). The Soerensen similarity, also known as Bray-Curtis or Czekanowski similarity, is a proportion coefficient in city-block space. As compared to Euclidean distance it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune & Mefford 1999). Considering the first 10 dominant species in cereal fields, the distance between fields in terms of species composition (1-Soerensen similarity) showed no significant relationship to the geographical distance for either sampling methods (Mantel test, suction sampling: $n = 4$, $R = 0.19$, ns, pitfall: $n = 6$, $R = 0.35$, ns, McCune & Mefford 1999), thus no regional effect on agrobiont composition can be inferred. The uniformity of agrobiont composition seems to be a generality that is valid for a

limited geographical area, such as Hungary. In this study only “arable agrobionts” are considered, but the identity of “agrobionts” is also strongly crop dependent. Different agrobionts can be found in structurally or otherwise radically different systems, such as orchards (Jenser et al. 1999) or rice (unpublished data), but within a range of only broadly similar crops, such as in alfalfa and cereals in the present study, no difference in the agrobiont composition could be shown. The agrobiont nature of individual species also shows geographical variation. Comparing the present data set with data of agrobionts in other European studies (Hänggi et al. 1995), for Central-Europe, four core arable agrobionts could be identified: *Meioneta rurestris* (C.L. Koch 1836), *Pachygnatha degeeri* Sundevall 1830, *Oedothorax apicatus* (Blackwall

Theridiidae life cycles

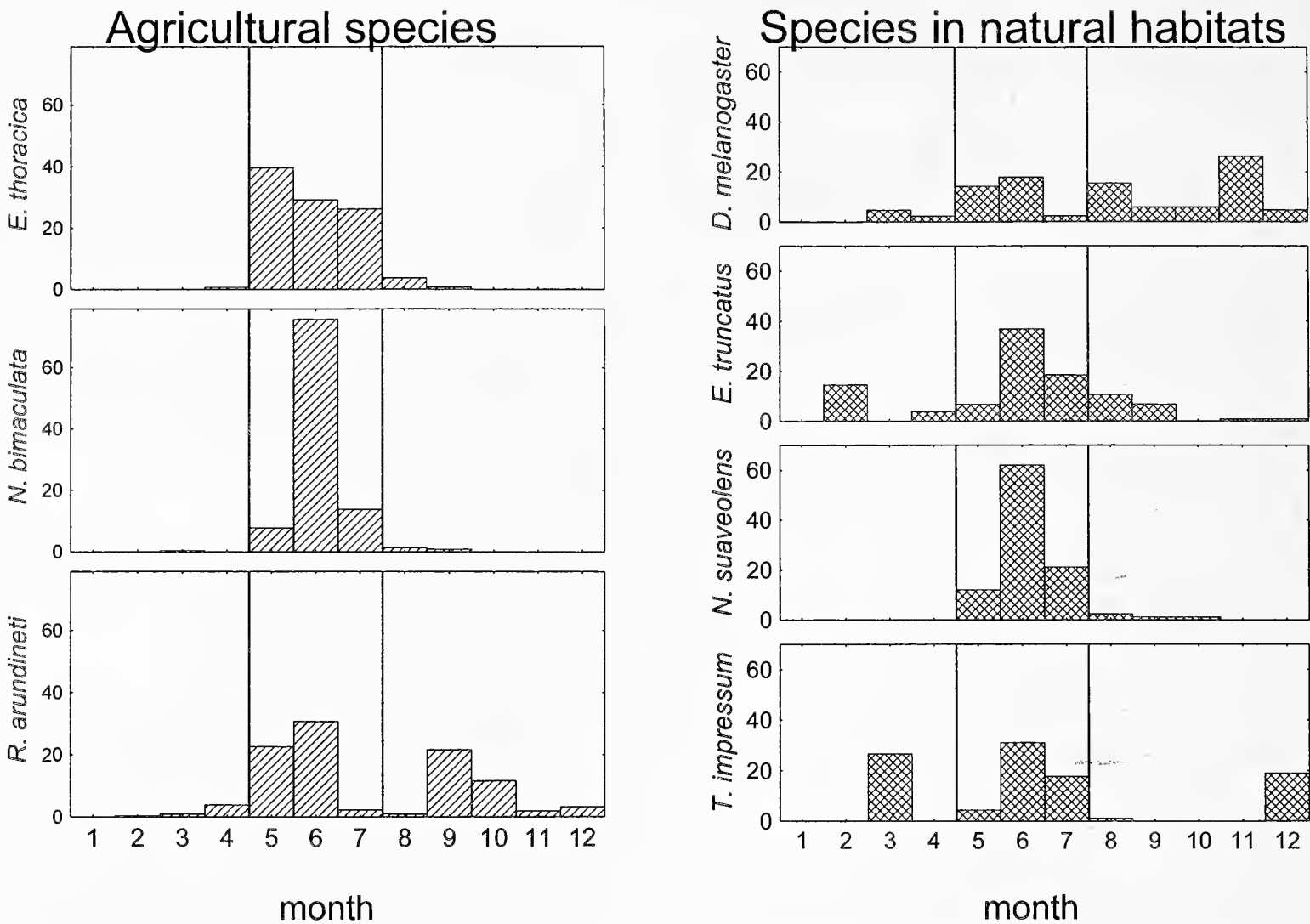


Figure 7.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Theridiidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Enoplognatha thoracica*, *Neottiura bimaculata*, *N. suaveolens*, *Dipoena melanogaster*, *Episinus truncatus*, *Theridion impressum*.

1850) and *Erigone dentipalpis* (Wider 1834). Other species, like the most abundant in Hungary, *Pardosa agrestis* (Westring 1861), show a strong North-West South-East geographical gradient in their association with agricultural systems (Blick et al. 2000). One of the major agrobionts of North-West Europe, *Lepthyphantes tenuis* (Blackwall 1852) shows an opposite gradient, and can be listed only as an agrophile in Hungary. *Pardosa agrestis* has a shift in life cycle along the same gradient; it has one generation per year in Northern Europe (S. Toft pers. comm.), and has two generations in Hungary (Samu et al. 1998). This parallel change in life cycle and agrobiont tendency suggests again the importance of life history characteristics for being successful in agricultural systems.

Habitat preference of agrobionts.—In Hungary agrobionts (first eight species of Table 2) were virtually only dominant in arable

fields. In secondary grassland habitat patches they represented a modest portion (13.6%) of the total spider fauna, and their overall presence was minimal (6%) in all studied natural grassland habitat types (Fig. 4). The indicator species analysis showed, that agrobiont species are not widespread generalists, that would occur in a wide range of habitat types. If agrobionts were wide-tolerance, eurytopic generalists, then they should not be indicators of either of the considered main habitat types. This hypothesis was falsified by finding that in all arable-grassland comparisons nearly all agrobionts showed up as indicators of the agricultural habitat (Table 3). On the other hand, indicator species analysis, by not providing any agrobiont as an indicator in the alfalfa-cereal comparison, reinforced the finding of the field-by-field comparison, that the same dominant species occurred in all arable fields, irrespective of crop type.

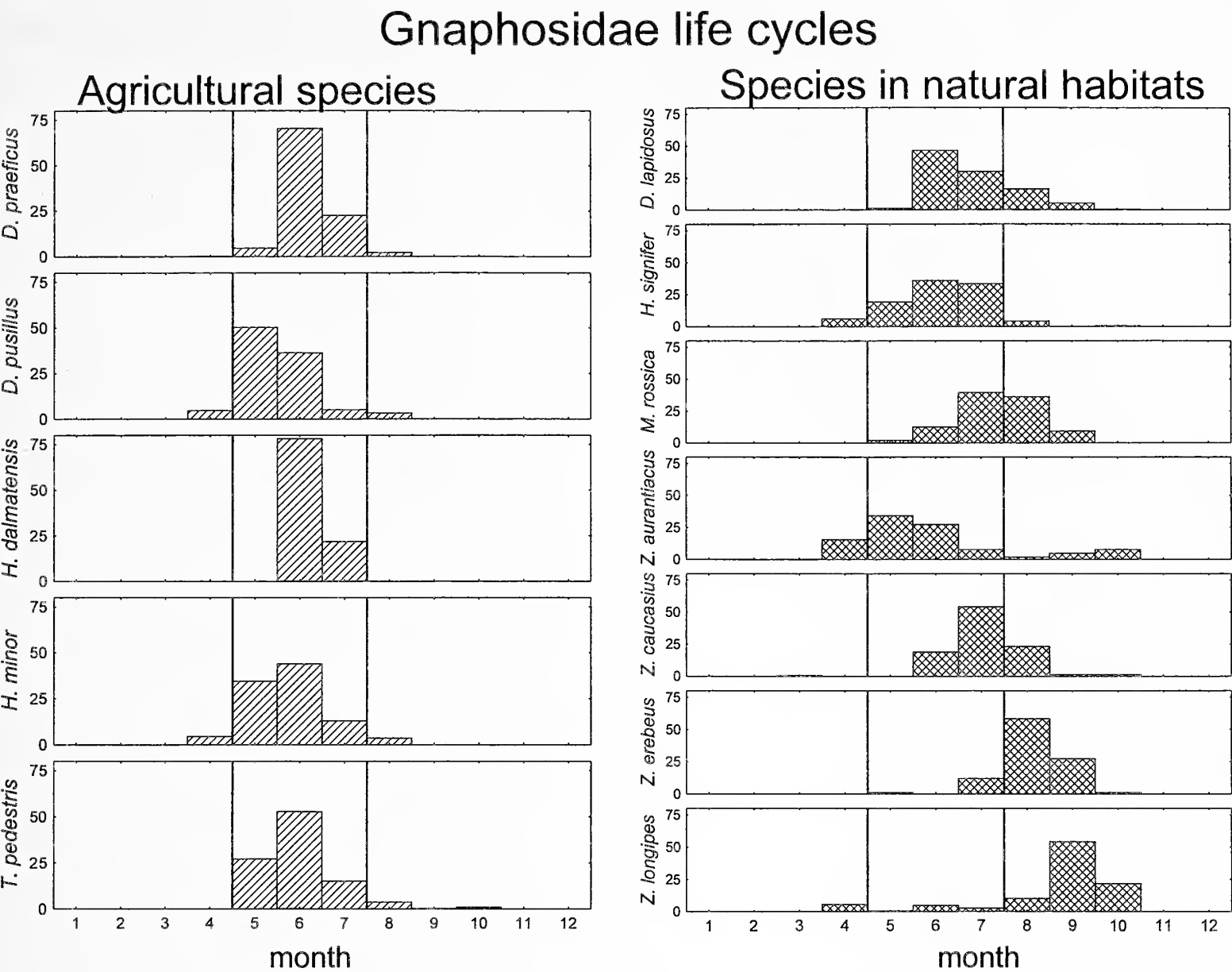


Figure 8.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Gnaphosidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Drassyllus praeficus*, *D. pusillus*, *Drassodes lapidosus*, *Haplodrassus dalmatensis*, *H. minor*, *H. signifer*, *Micaria rossica*, *Trachyzelotes pedestris*, *Zelotes aurantiacus*, *Z. caucasicus*, *Z. erebeus*, *Z. longipes*.

The scope of the present study was not wide enough to indicate the full range of natural habitats agrobionts occupy. We have extracted the habitat preferences of nine agrobiont species from Hänggi et al.'s (1995) database of Central European spiders (Table 4). These data are from the literature, and encompass a wide range of different habitats. The survey shows that, taking this broader view, agricultural habitats are still the most preferred ones for agrobionts. We think that both the Hungarian data (Fig. 4) and the data in Table 4 show that it cannot be stated as a general rule, that agrobionts are originally hygrophilous species that are native in littoral areas (Raatikainen & Huhta 1968; Luczak 1979). In our view, the essence is not the hygric nature of the native habitat; the disturbance pattern is more important. From the Eu-

ropean survey it emerges that agrobionts are abundant in abiotically driven, frequently disturbed and/or pioneer areas, but they are less frequent in mesic, stable habitat types.

The APEH hypothesis (Wissinger 1997) concerns the adaptedness of agrobiont invertebrates, and makes a specific prediction about the disturbance pattern in their native habitat, namely that they originate from predictably ephemeral habitats. *Pardosa agrestis* in Hungary seems to provide a nice case for APEH, because its main natural habitats are saline marshes (Szita et al. 1998) that are annually flooded during the spring and autumn rainfall maximums, and are dry in between. Both disturbance periods coincide with the presence of small-medium sized juveniles, the possible colonizer stage (Richter 1970), while the species is known to reproduce in June (and also

in August), during the relatively stable period in its habitats. This again draws our attention to the importance of life cycle synchronization with habitat and landscape dynamics.

Life cycle of agrobionts.—To study life history adaptation of agrobionts to arable systems, we chose more species than the first 10 most dominant ones. We selected species from the four most prevalent families present in Hungarian arable systems (Lycosidae, Linyphiidae, Gnaphosidae and Theridiidae) by the criteria that they showed a clear preference for either arable or natural habitat types, and we possessed enough data to plot adult phenology (Figs. 5–8). Phenology curves showed that species occurring in natural habitats, in all four families, had a more varied phenology. Although agricultural species showed variation, they considerably synchronized their first generation with the main vegetation period of arable crops (which in Hungary is May–July). The onset of the favorable size of the crop (May) seemed to be the strongest factor that limited the energy, and therefore prey demanding maturation and reproduction for most agricultural species. None of the 18 species we examined had an adult peak before May, while 6 of the 22 species from natural habitats had an early spring adult peak. Some agricultural species could make use of the post harvest period by producing a second generation (e.g., *Pardosa agrestis* and *Robertus arundineti*). Some Linyphiidae species are known to have multiple generations per year (Topping & Sunderland 1998). Here the main peak also coincided with the May–July period, but adults seemed to be present somewhat earlier, as well as later on in the year.

Synchronization with habitat changes was also noted by Toft (1989). During the main crop growing period, May–July, environmental conditions are fairly stable, the maturing crop provides sufficient prey and shelter from abiotic disturbances. Such a life cycle pattern supports the APEH hypothesis. Agrobionts make use of the predictably occurring good period by maturing and reproducing during that time. Arable habitats are likely to be colonized by younger instars (by most families, except for Linyphiidae) and dispersed from in late summer and autumn. A literature survey shows (Sunderland & Samu 2000) that field margins and hedgerows provide fewer colonizers, and population movements are likely

to be between fields of different crops and/or management stages.

CONCLUSIONS

Based on ten years of survey data on Hungarian arable field spider communities, we can generalize both about the structure of agricultural spider communities and about the ecological nature of their most dominant species, the agrobionts. We found that the skewed dominance structure of agricultural communities is invariable both in our data sets and in the literature. The skew is caused by the over-dominance of a few agrobionts; typically less than 10 species make up 60–90% of the whole spider community. The remaining part of agricultural communities was rather variable, causing large differences in species richness values in individual fields. Nevertheless, a high diversity of spiders in arable fields was detected, which might have implications in conservation.

The agrobiont segment of arable spider communities showed very little field-by-field variation, and within Hungary no regional effects could be detected. Agrobiont species were always the most dominant in agricultural habitats, and occurred only sporadically in natural habitats, thus they can be regarded as specialists of the agricultural habitat type. For larger geographical regions, even if the potential species pool were the same, climate related life history variations might cause different species to become successful agrobionts in certain regions, and to be absent from agricultural communities in others. Agrobionts, by and large, came from frequently disturbed, pioneer, or otherwise abiotically driven habitats, but the usually not very clear (and regionally also potentially variable) habitat preference of agrobionts makes it difficult to test specific theories, like APEH, except for certain well studied species. The life cycle of agrobionts and agrophile species nearly unequivocally showed synchronization with the main crop growth period, which provides indirect support for the APEH hypothesis.

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THE INFLUENCE OF MOUND STRUCTURE ON THE DIVERSITY OF SPIDERS (ARANEAE) INHABITING THE ABANDONED MOUNDS OF THE SNOUTED HARVESTER TERMITE *TRINERVITERMES TRINERVOIDES*

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ABSTRACT. The dynamics of spiders present in abandoned *Trinervitermes trinervoides* (Sjöstedt) termite mounds were studied over a period of one year, from March 1999 to January 2000, with five mounds excavated on a bimonthly basis. All spiders present in the mound were collected by hand and preserved in 70% ethanol. A total of 771 spiders represented by 21 families and 82 species were collected from the 30 mounds during the course of the study. The most abundant were the Gnaphosidae, which represented 37.87% of all spiders collected, followed by the Salticidae (12.97%), Pholcidae (10.51%) and Oonopidae (9.60%). These were the only families that represented more than 5% of the spider fauna. The most abundant species were *Zelotes fuliginus* (Purcell 1907) (Gnaphosidae) (11.69%), *Smeringopus sambesicus* Kraus 1957 (Pholcidae) (10.51%), *Heliophanus* sp. (Salticidae) (9.86%) and a Gamasomorphinae sp. (Oonopidae) (9.21%). A correlation was found between spider abundance and mound height, surface perforation of the mound and season of collection. Spider numbers were highest in mounds with a high surface degradation, while a tendency existed for an increase in numbers with increased mound height. Web-building spiders (Pholcidae and Theridiidae) were largely limited to mounds with a cavity in the structure.

Keywords: Termite mounds, spiders, mound structure

Knowledge of the spiders in southern Africa is largely limited to species descriptions, while their ecology remains relatively unexplored. However, during the last two decades there has been an increase in research into the diversity and ecology of spiders in southern Africa. Research on spiders in natural habitats has addressed diversity in grassland (Lotz, Seaman & Kok 1991), savanna (Dippenaar-Schoeman, van den Berg & van den Berg 1989), Nama Karoo Biome (Dippenaar-Schoeman, Leroy, de Jager & van den Berg 1999), the fynbos biome (Coetzee, Dippenaar-Schoeman & van den Berg 1990), pine plantations (van den Berg & Dippenaar-Schoeman 1988), and indigenous forests and pine plantations (van der Merwe, Dippenaar-Schoeman & Scholtz 1996).

The research on the association of spiders with termites in southern Africa has thus far

only involved two widespread termite species, namely the harvester termite *Hodotermes mossambicus* (Hagen), dealt with by Dippenaar & Meyer (1980), van den Berg & Dippenaar-Schoeman (1991), Jocqué & Dippenaar-Schoeman (1992), and Dippenaar-Schoeman, de Jager & van den Berg (1996 a,b), and the fungus growing termite *Odonotermes transvaalensis* (Sjöstedt), investigated by Cumming (1993) and Wesolowska & Cumming (1999).

Until now the spiders associated with the mound-building snouted harvester termite *Trinervitermes trinervoides* (Sjöstedt) have not been investigated. This termite species is particularly abundant in the grassland and savanna regions of central South Africa, and constructs dome-shaped mounds (Meyer 1997). The death of a queen and subsequent deficiency of a successor has the effect of the col-

ony declining in number as no more progeny is produced to replace termites that die or are preyed upon (R. Adam, pers. comm.). The queen's death never has the consequence of immediate mass mortality of the colony, but in most cases "abandoned" mounds do contain termites, mainly workers, which are remnants of the colony that previously occupied the mound. Ultimately the mound will become a dead structure with no termites. Abandoned *T. trinervoides* termite mounds form an important part of the grassland ecosystem in the Free State, serving as a refuge for a wide variety of vertebrates (reptiles and mammals) and invertebrates (spiders, scorpions, mites and insects). The mounds are slowly degraded by weathering and the digging of termitivorous mammals such as *Orycteropus afer* (aardvark), exposing the mound surface to colonization by such opportunistic organisms.

The interaction between the spiders and the termites varies and three possible interactions exist: termitophilous species, which reside permanently in the termite mound; spiders that live in close association with the termites and prey on them, also known as termitophages; and spiders that use mounds as a shelter and for occasional food. The latter case will be dealt with here. This is the second study on spiders of grassland in the Free State, South Africa and the first of three papers reporting on spider diversity associated with the abandoned mounds of *T. trinervoides*. This study forms part of the South African National Survey of Arachnida (SANSA).

METHODS

Study area and period.—The farm Deelhoek is situated approximately 38 km northwest of Bloemfontein (28° 54' S, 26° 07' E) in the Free State at an elevation of approximately 1250 m. The farm comprises 350 ha of cultivated lands and 768 ha of grassland dominated by *Themeda triandra*, *Cymbopogon* and *Eragrostis* grasses. The farm falls within the summer rainfall region of South Africa, with the annual rainfall averaging 400–500 mm. The mounds studied were located in the grassland section of the farm, which contained a red soil substrate with a partially rocky composition in the northern and eastern parts. The spiders in the abandoned termite mounds were studied over a period of 11 months from March 1999 to Jan-

uary 2000, with five mounds excavated on a bimonthly basis to search and locate all spiders sheltered within.

Mound parameters.—A brief description of the mound (height and degree of perforation of the exterior surface), the condition of the surrounding grassland, as well as the weather conditions was made prior to the excavations.

Degree of perforation (DOP) describes the degree of disintegration of the outer surface of the mound either by weather conditions such as wind and rain, or by digging actions of aardvark or other termitophagous mammals. Such weathering would typically be repaired if an active colony was residing in a mound, but once the queen has died, no repairs are done and the structure gradually breaks down. A value was assigned to each mound depending on the proportion of the surface with exposed tunnels. A higher percentage value indicates a more advanced stage of disintegration. A DOP of 100% indicates a mound with a minimal number of tunnels remaining exposed to the outside and the majority of the exterior surface disintegrated and sandy. A DOP of 90% shows that the exterior of the mound has started to break up or disintegrate. A DOP of 80% indicates that the entire surface of the mound is weathered and the tunnels in the mound are all exposed to the environment outside the mound. As this represents the entire surface of the mound (8/8), mounds with a DOP of 70% and less have a relative proportion (in eighths) of the surface weathered with exposed tunnels. For example, mounds with 60% DOP have 6/8 of the surface with exposed tunnels, etc.

The height of the mound was measured with a meter rule. Mound height is important in determining the amount of living space available to the mound inhabitants. The presence or absence of cavities in the mound structure further affects the volume of living space and distribution of organisms due to niche variation, while at the same time providing a microhabitat for occupation by sedentary web-building spiders. Cavities are typically hollow spaces within the mound structure or on the outside of the mound where mammals have dug, and are usually greater than 0.5 dm³ in volume. In comparison, tunnels are at the very most 12 mm in diameter.

Collecting methods.—Five mounds were dug open in their entirety during each of the six sampling periods using a pitchfork. Mounds were randomly selected, but emphasis was placed on trying to excavate mounds of different heights and DOP. Excavation began with the dome of the mound and proceeded to the tunnels beneath the ground level. Sections of the mound were broken into smaller pieces so that the tunnels could be examined to collect all spiders with an aspirator or jar in 70% ethanol. Notes were also made on the non-aranean fauna inside the mound, with special reference to the quantity of termites remaining in the mounds. Following excavation an estimate of the remaining termite population was made (calculated as a percentage of an active colony in a mound of the same size). If any cavities were present in the mound structure an estimate of their volume (in dm³) was made.

Due to taxonomic problems within some families and the high number of immatures collected, numerous specimens could only be identified to generic, or in a few cases, to family or subfamily level. Voucher specimens have been deposited in the National Collection of Arachnida at ARC- Plant Protection Research Institute in Pretoria, South Africa.

RESULTS AND DISCUSSION

Numbers and species present.—A total of 771 individuals were collected from the 30 mounds representing 21 families and 82 species (Table 1). The most abundant family was the Gnaphosidae representing 37.87% of the total number of spiders, followed by the Salticidae (12.97%), Pholcidae (10.51%) and Oonopidae (9.60%). These were the only families that represented more than 5% of the spider fauna.

The most abundant species were *Zelotes fulgineus* (Purcell 1907) (Gnaphosidae, 11.69%), *Smeringopus sambesicus* Kraus 1957 (Pholcidae, 10.51%), *Heliophanus* sp. (Salticidae, 9.86%) and a Gamasomorphinae sp. (Oonopidae, 9.21%). These were the only species constituting more than 5% of the total. Twenty-one of the 82 species (25.6%) were represented by single individuals. A greater diversity of spiders was collected in this study compared to a study on spiders associated with the harvester termite *Hodotermes mos-*

Table 1. Family composition of spiders collected from *Trinervitermes trinervoides* mounds on the farm Deelhoek, Bloemfontein, showing abundance and species diversity from thirty mounds sampled.

Family	Total collected	% of Total	Total species	% of Total
Ammoxenidae	5	0.65	1	1.22
Agelenidae	2	0.26	1	1.22
Caponiidae	18	2.34	1	1.22
Corinnidae	10	1.30	4	4.88
Ctenizidae	3	0.39	1	1.22
Dictynidae	1	0.13	1	1.22
Eresidae	5	0.65	1	1.22
Gnaphosidae	292	37.87	29	35.37
Hahniidae	1	0.13	1	1.22
Linyphiidae	21	2.72	2	2.44
Liocranidae	32	4.15	5	6.10
Lycosidae	10	1.30	5	6.10
Mimetidae	3	0.39	1	1.22
Oonopidae	74	9.60	2	2.44
Palpimanidae	5	0.65	3	3.66
Philodromidae	4	0.52	2	2.44
Pholcidae	81	10.51	1	1.22
Prodidomidae	38	4.93	6	7.32
Salticidae	100	12.97	7	8.54
Theridiidae	34	4.41	6	7.32
Zodariidae	32	4.15	2	1.22
Σ	771		82	

sambicus, in which 55 species were collected (van den Berg & Dippenaar-Schoeman 1991).

Van den Berg & Dippenaar-Schoeman (1991) found that gnaphosids represented 20.0% of the species in an area where *H. mosambicus* was found. In this study the gnaphosids were also the most diverse family, accounting for 35.37% of the species collected (Table 1). This indicates that gnaphosids often represent the most diverse and abundant group of spiders in the grassland biome in southern Africa (see also Lotz et al. 1991).

Spiders in web building families are more likely to remain in the mounds for a longer period of time following construction of their webs, e.g. *S. sambesicus*. Communal webs of this species were observed in single termitaria for as long as 6 weeks.

Ground wanderers, which were more abundant, are for the most part active hunters and the more common species may forage within the mound and its surroundings. Rare species may accidentally wander in and out of the mound, or use it as an overwintering facility. The salticid *Heliophanus* sp. and Gamaso-

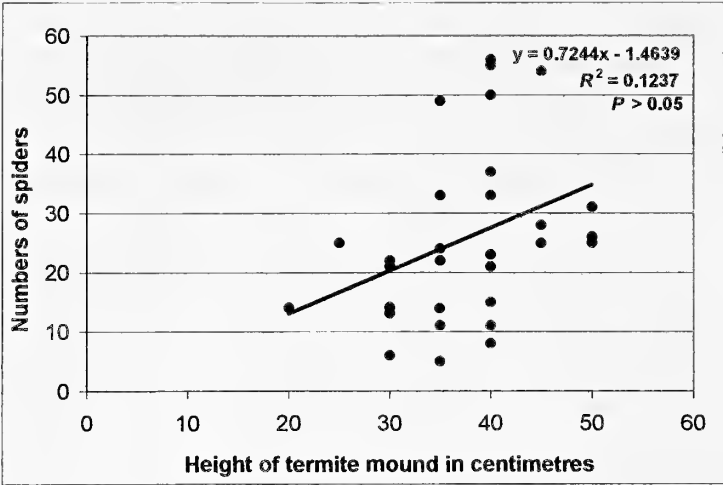


Figure 1.—Linear regression of total spider numbers versus the estimated height (in centimeters) of abandoned mounds of the termite *Trinervitermes trinervoides*, sampled between March 1999 and January 2000 at Deelhoek, Bloemfontein.

morphinae sp. (Oonopidae) appear to be the only species collected that are specifically associated with these abandoned mounds, as they were neither collected on grass or in pit-falls in the surrounding grassland. These two were of the most abundant species collected, and also represent the bulk of the individuals collected from each family, i.e. 76.0% and 97.3%, respectively. Nothing is presently known about the means by which the mounds are located by these spiders.

Influence of mound height on abundance.—The spider abundance in the 30 mounds sampled was plotted against the mound height measured prior to sampling, and a linear trendline extrapolated (Fig. 1). Despite the uneven distribution of the mound heights, the majority being between 30 and 40 cm high, the linear progression shows that with an increase in mound height there is an increase in spider abundance. This is to be expected as the mounds of *T. trinervoides* take

the shape of a dome (Meyer 1997), and consequently the slightest difference in height has a fairly significant influence on the surface area and volume of the mound. However, the highly variable numbers of spiders encountered within a given height range make it difficult to accurately predict the spider abundance for a specific height. Although expected to be a major influence on spider abundance, this relationship was found to be not significant ($R^2 = 0.1237$, $P > 0.05$). The maze-like interior of the mound may make it difficult for spiders to find their way out once they have entered the mounds, especially in the case of ground wanderers such as gnaphosids that are not specially adapted the mound habitat. The exception may be the two likely specialists mentioned above, which have probably adapted to negotiate their way around the mounds successfully.

Influence of degree of perforation.—The mean numbers of spiders per mound were highest in mounds with a DOP of 60–80% (Table 2), with numbers considerably lower when the surface was severely degraded (DOP's of 90–100%). A combination of a substrate of loose sand (which may not be as suitable as a firm surface for ground wandering spiders with running-hunting lifestyles that have to search for their prey) and a low number of exit holes may result in spiders not even entering such mounds. Numbers were also low when the number of entrance holes were minimal ($\leq 50\%$). The high number of exposed tunnels and hard surface at DOP's of 60–80% is probably responsible for the highest spider abundance in these mounds.

To determine the effect that degree of perforation (DOP) had on spider abundance it was necessary to consider the effect of mound

Table 2. Analysis of the relationship between mound height and spider abundance for six categories of degree of perforation (DOP) of abandoned *Trinervitermes trinervoides* mounds at Deelhoek, Bloemfontein.

Degree of perforation	50%	60%	70%	80%	90%	100%
Number of mounds	4	5	5	6	5	5
Mean mound height	41.25	42.00	37.00	36.67	36.00	33.00
Number of spiders	72	175	156	170	83	105
Mean spiders per mound	18.00	35.00	31.20	28.33	16.60	21.00
Standard deviation	8.52	19.25	13.07	20.95	9.71	5.70
Ratio of mean spiders: mean mound height	0.44	0.83	0.84	0.77	0.46	0.64

height as well. By calculating the relationship between mean mound height and spider abundance for each of the six categories of DOP sampled, a similar pattern emerged: numbers of spiders are highest at DOP's of 60–80%, irrespective of the height of the mounds (Table 2).

Cavities in the mound structure.—Web-building spiders (e.g. Pholcidae and Theridiidae) were largely limited to mounds with a cavity in the structure. Most web-building families (e.g. Agelenidae, Dictynidae, Eresidae, Hahniidae and Linyphiidae) were found in tunnels inside the mounds, while pholcids and theridiids were found in cavities in the center or on the outside of the mound structure. Numbers of *S. sambesicus* showed no relationship to season but may be affected by the life cycle of the species. The highest number of *S. sambesicus* collected from a single mound was 38 specimens, 31 of which were immatures. It appears that if the cavity is large enough immatures will remain in a particular mound and co-exist on a social basis, sharing a common web and possibly feeding together on prey caught in the web. It is presently not known whether some of the spiders will leave a particular mound as they approach adulthood, not only due to increased intraspecific competition for food and spatial resources, but also for reproductive purposes.

Heidger (1988) found that *Smeringopus pallidus* (Blackwall 1858) co-inhabits abandoned mammal burrows together with two other web building spiders, *Olorunia ocellata* Pocock 1900 (Agelenidae) and *Euprosthénops proximus* Lessert 1916 (Pisauridae), and may display kleptoparasitic behavior in view of the weak criss-cross threads that it constructs above the webs of the two other species. The webs of *S. pallidus* are too weak to catch large insect prey. In the case of *S. sambesicus* inhabiting abandoned *T. trinervoides* termitaria, however, the webs were relatively dense, and as no other web builders were present, this species is able to catch its own prey and does not rely on a kleptoparasitic lifestyle for survival.

The numbers of *S. sambesicus* were highest in mounds in which the cavity was located on the outside of the mound or was linked to the outside by a space, as opposed to a hollow in the center of the mound structure. A pholcid

would struggle to navigate its way along the narrow tunnels to a cavity inside the mound.

Presence of termites.—High *T. trinervoides* densities (maximum of 40%) in abandoned mounds seemed to negatively affect the densities of spiders, probably due to the repellent chemicals produced by soldier termites. Spider numbers were generally highest at low densities of *T. trinervoides*. This was especially prevalent in the case of the *Heliophantus* sp., which was most abundant at termite densities below 5%, but absent at high termite densities (> 45%).

The five *Ammonoaxenus amthalodes* Dippenaar & Meyer 1980 (Ammonoaxenidae) specimens were all collected from mounds secondarily occupied by *H. mossambicus* ($n = 6$). As these spiders are known to be specialist predators of *H. mossambicus* (Dippenaar-Schoeman, et al. 1996 a, b), secondary occupation of these abandoned mounds by this termite is likely to be coupled with the presence of these spiders.

Spiders are among the most common and diverse groups of invertebrates colonizing abandoned *T. trinervoides* termite mounds. The height and degree of surface degradation of the mounds, and the presence of cavities in the mound structure are some of the factors influencing spider diversity and abundance. Spiders are possibly the most common and frequently encountered invertebrate predators inhabiting abandoned mounds.

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COMPARISON OF AUTUMN AND WINTER DEVELOPMENT OF TWO WOLF SPIDER SPECIES (*PARDOSA*, LYCOSIDAE, ARANEAE) HAVING DIFFERENT LIFE HISTORY PATTERNS

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ABSTRACT. *Pardosa* species do not overwinter in the adult stage in the Holarctic region, therefore penultimate instars should avoid precocious maturation in autumn. We tested how artificially increased temperature and/or lengthened light regime would affect the pre-overwintering development of two common species with different phenological patterns. Juvenile instars of *Pardosa agrestis* (Westring 1861) and *P. hortensis* (Thorell 1872) were collected in autumn from the field. The experimental spiders were held either indoor at 26 °C or outdoors at ambient temperature and were exposed either to short or to long daylength. Molting events were monitored for five months. At outdoor temperatures no spiders reached adulthood and molts of younger instars occurred more frequently at long daylength. In the indoor temperature groups all *P. hortensis* and the majority of *P. agrestis* individuals reached adulthood during the experiment. Long daylength treatment enhanced the effect of increased temperature by almost halving the time needed to reach adulthood in both species. Penultimate instars of both species needed at least 17 days to molt, while earlier instars, present only in *P. agrestis*, responded rapidly to higher temperature by molting. This stage dependent response suggests that earlier instars can use favorable autumnal temperatures to catch up with penultimate instars which leads to higher synchrony of developmental stages in the overwintering and spring populations.

Keywords: Life history, overwintering, diapause, stenochronous, wolf spider

Pardosa species reach high population densities in a number of habitat types, including agricultural habitats, all over the world. In the Holarctic region most of the species are stenochronous with spring–summer reproduction, overwintering as immature instars. However, some species have a rather flexible life history pattern—being biennial, annual–biennial or having a one year life cycle depending on latitude (Edgar 1972; Stepczak 1975) or the primary productivity of the habitat (Schmoller 1970). There are also indications that certain species may have two generations per year in more southern latitudes (Miyashita 1969; Samu et al. 1998). In spite of this flexibility in life history pattern and the significant winter activity observed in some species (Aitchison 1984), no *Pardosa* species were found to overwinter in adult stage.

For this experiment we chose two common *Pardosa* species: *Pardosa agrestis* (Westring 1861) and *Pardosa hortensis* (Thorell 1872). There is a clear difference in the habitat preference of the two species. Although both of them can be found together in most of the

agricultural habitats in Hungary, *P. hortensis* can reach extreme dominance among cursorial spiders in gardens and grass-covered vineyards (Kiss pers. obs.), while *P. agrestis* is by far the most abundant spider species in arable fields (Samu et al. 1996; Tóth 1999). The two species have different phenological patterns in Hungary. *Pardosa hortensis* has one reproductive period in spring (in April–May), while *P. agrestis* adults have two separate peaks a year (in May–June and in August) (Samu et al. 1998; Samu & Szinetár in press).

Since adult individuals in the genus *Pardosa* seem to be unable to overwinter, the regulation of the autumnal development of immature individuals is of pronounced importance to avoid untimely maturation before winter, especially in geographical areas with unpredictable warm periods in autumn. In contrast with the numerous publications on life history patterns of *Pardosa* spp., surprisingly few manipulative studies have investigated the factors determining their pre-overwintering development. In his comprehensive study Schaefer (1977) assumes that in spiders,

similar to insects, photoperiod and temperature are the principle factors in the evocation and termination of the dormancy. In the sporadic studies on the dormancy phenomenon in spiders two types of dormancy, quiescence and diapause, are generally distinguished. Quiescence is a simple retardation of development due to the unfavorable level of some physical factor (e.g. temperature), which can be resumed without delay by favorable changing of that factor. In contrast with quiescence, the state of diapause imply basic changes in the hormonal status of the spider, thus diapause cannot be immediately released by favorable changing of the inducing environmental factor (Schaefer 1977). In some stenochronous species reproducing in spring and summer, low temperatures as well as short daylengths were shown to retard the development of immature individuals. The mechanism of this retardation can be the prolongation of intermolt cycles and, in some cases, the increasing of the number of instars (Schaefer 1976). Miyashita (1969) found a strong inhibition of molting in penultimate instars of *Pardosa astrigera* L. Koch 1878 collected at the beginning of the overwintering season from the field. The inhibition was persistent even in warm conditions with long day length. Schaefer (1987) has shown that penultimate instars of the wolf spider *Pirata piraticus* (Clerck 1757) overwinter in diapause, while younger juvenile stages in quiescence. In the present study we tested how different temperature and daylength affects the development of the pre-overwintering individuals of two common *Pardosa* species having different phenological patterns.

METHODS

Immature *Pardosa agrestis* and *P. hortensis* individuals were collected respectively from an alfalfa field dominated by *P. agrestis* on 30 September 1998 and from an abandoned garden dominated by *P. hortensis* on 10 October 1999, near Budapest (Hungary). Spiders were collected individually regardless of their size, thus representing the approximate size distribution of the population on the site at the date of collection. The spiders were placed in separate plastic vials (diameter = 3 cm; height = 6 cm) with moistened plaster of Paris on the bottom. The vials with spiders were randomly assigned to one of four light boxes represent-

ing either of the four treatments arising from two temperature groups (outdoor/indoor) and two levels of light regime (light:dark 16:8 and 8:16). All the four treatment groups of *P. hortensis*, and the two outdoor temperature groups of *P. agrestis* started with 50 animals, while in the case of *P. agrestis* the two indoor temperature groups started with 75 spiders. The light boxes ensured a free air flow from the outside, thus the temperature within the boxes was the ambient temperature (indoor or outdoor) hourly recorded by data loggers. The light was provided by neon gas lighting tubes controlled by timer switch for each box. The tubes were isolated by a transparent glass from the inside space of the boxes to avoid light dependent heating effect. The two boxes of the outdoor temperature groups were placed inside a chicken wire sided garden-shed, thus the temperature followed natural-like daily curves. The boxes of the indoor temperature groups were placed in a room with controlled temperature. To ensure a daily temperature rhythm, the constant 26 °C temperature was lessened to 18 °C for 4 h each day in the middle of the dark period. The cooling procedure took ca. 30 min, while 5 min were needed to reach the 26 °C again. The spiders received fruit flies (*Drosophila melanogaster*) *ad libitum*. Checks for molting took place three times a week. The experiments ended on 1 March both years.

Two statistical methods, Gehan's Wilcoxon test (Gehan 1965) and proportional hazard (Cox) regression (Cox 1972), offered by the Survival and Failure Time Analysis module of the Statistica program package (Statsoft, Inc. 2000) were used to compare the tendency to molt and the tendency to reach adulthood of the spiders under different conditions. The main advantage of these methods, as compared to more generally used statistics, is that "censored" cases, in which we only know that the event in question did not occur before a given time, e.g. the experimental individual did not molt before the end of the experiment or before its death, can be analyzed together with "complete" cases, in which the event was actually observed and thus the complete time to the occurrence of the event was known. An other important point is that neither of the two methods have constraints concerning the distribution pattern of the underlying time periods.

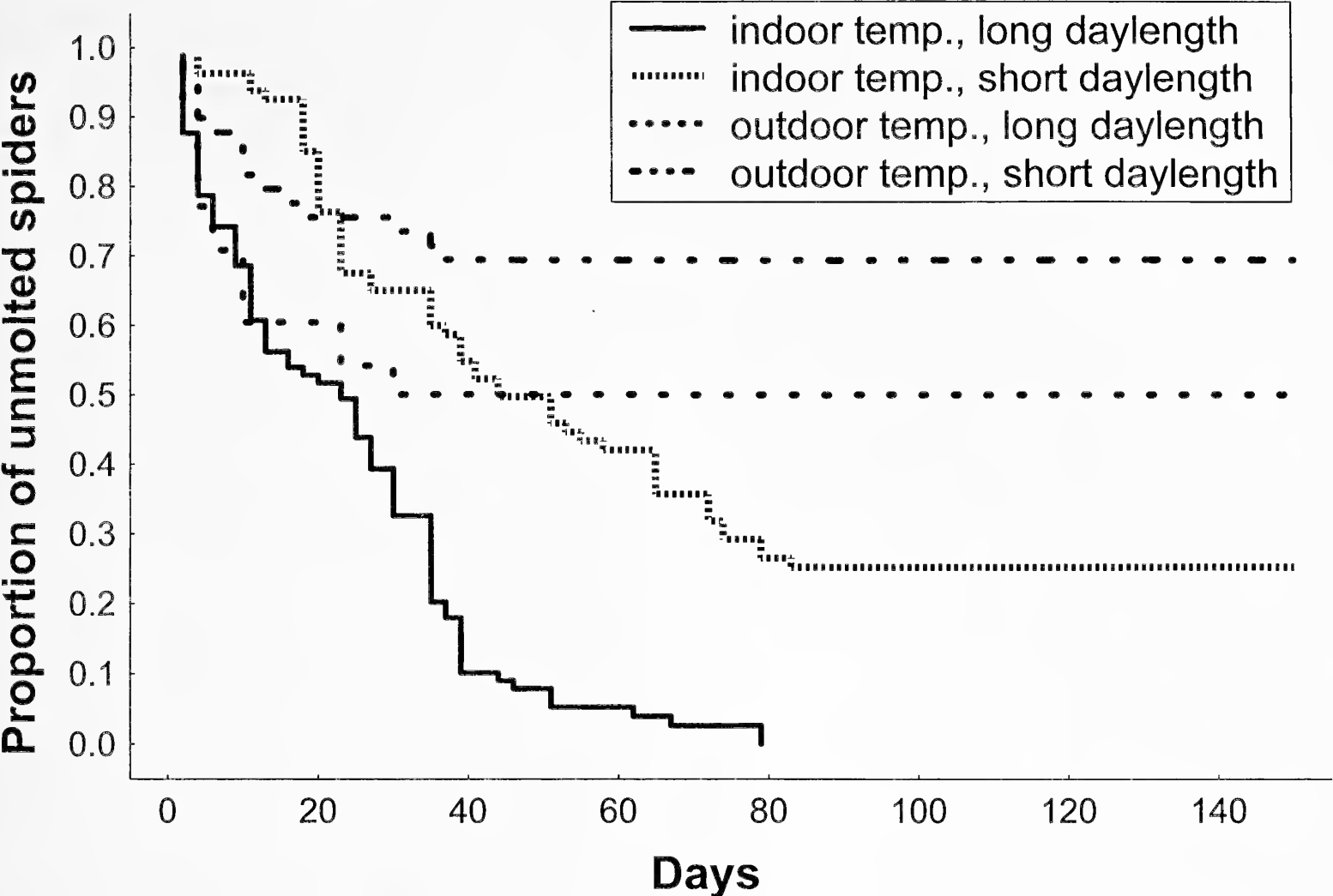


Figure 1.—Proportion of unmolted *Pardosa agrestis* individuals changing with time over the course of the experiment in the four treatments.

RESULTS

Outdoor temperature groups.—In the case of *P. hortensis* none of the immature spiders molted during the experiment, irrespective of the light regime. In *P. agrestis* 24 and 15 individuals molted at long and at short daylength respectively, the spiders molted significantly sooner at long than at short daylength (Gehan’s Wilcoxon test: $Z = -2.15$, $P = 0.031$). No individuals molted more than once, and none of them became adult. The molting events ceased after 5 November, as the daily maximum temperature decreased and no longer reached 10 °C (Fig. 1). In the autumnal months only four experimental spiders were lost (1 *P. hortensis* and 3 *P. agrestis*), while during the winter months (December–February) the mortality rates were high (60 % in *P. hortensis* and 76 % in *P. agrestis*).

Indoor temperature groups.—*Pardosa hortensis*: No immature *P. hortensis* was left by the end of the experiment. Ninety-one individuals reached adulthood within 90 d, 86 of them in one, five of them in two molts. Nine of the 100 experimental spiders died be-

fore maturing. The first molting to adulthood occurred 17 d after the beginning of the experiment. The average time to reach adulthood was significantly longer at short day length (mean \pm SD: 64 ± 17.2 days) than at long day length (36 ± 15.1) (Mann-Whitney U test: $Z = -6.25$, $P < 0.001$). The proportion of males ($n = 49$) and females ($n = 42$) in the experimental animals did not differ significantly from 50%. In the regression model containing light treatment and gender as predictor factors gender had no significant influence on the time needed to reach adulthood (Proportional hazard (Cox) regression: $\chi^2 = 28.41$, $df = 2$, $P < 0.001$; effect of light regime: $t = -5.29$, $\beta = -1.27$, $P < 0.001$; effect of gender: $t = 1.14$, $\beta = 0.12$, $P = 0.255$) (Fig. 2).

Pardosa agrestis: Seven and 19 immature spiders were lost (died or escaped) before the end of the experiment at long and short daylength respectively. All of the surviving individuals became adults at long daylength ($n = 68$), while at short daylength 42 of the 56 spiders molted at least once, and 38 of them

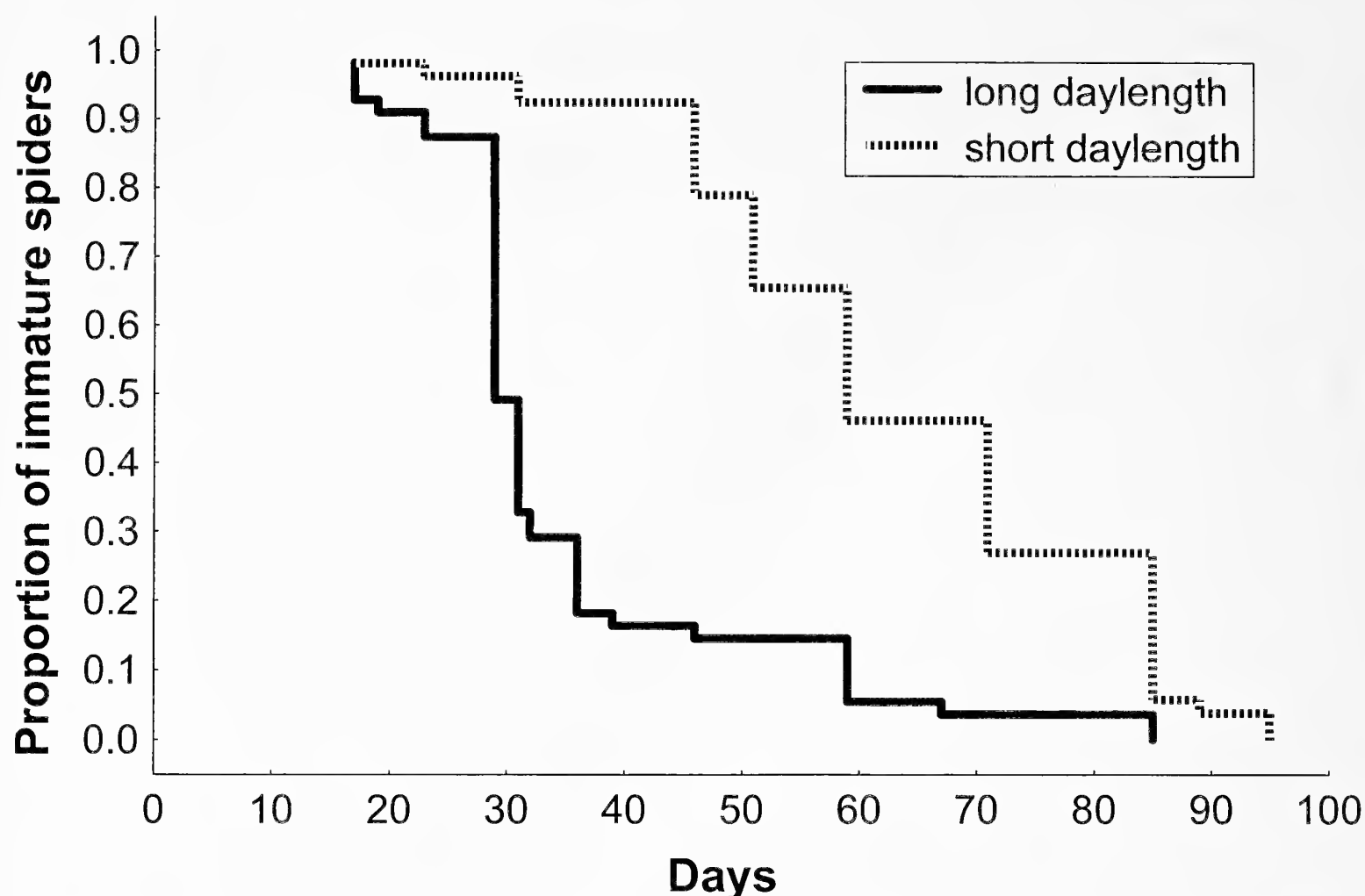


Figure 2.—Proportion of immature *Pardosa hortensis* individuals changing with time over the course of the experiment under different light regimes at indoor temperature.

reached adulthood. One to four molts were needed to reach adulthood ($n = 15; 53; 31; 7$); the distribution of the number of molts needed did not differ significantly between the light regimes (Correspondence analysis $\chi^2 = 0.19$, $df = 3$, $P = 0.979$). In the adults, the proportion of males ($n = 50$) and females ($n = 56$) did not differ significantly from 50%. The time to reach adulthood at short daylength (mean \pm SD: 84 ± 17.1 d) and at long daylength (55 ± 31.5 d) naturally depended on the number of molts needed, but more importantly it significantly depended on the light regime, but not on gender (Proportional hazard (Cox) regression: $\chi^2 = 26.53$, $df = 3$, $P < 0.001$; effect of light regime: $t = -3.43$, $\beta = -0.76$, $P < 0.001$; effect of number of molts: $t = -3.95$, $\beta = -0.55$, $P < 0.001$; effect of gender: $t = -0.79$, $\beta = 0.16$, $P = 0.431$).

The length of the time to the first molt after getting into the laboratory was significantly influenced by the number of the further molts needed to reach adulthood and the light regime. Individuals of earlier stages molted sooner than later instars; spiders molted sooner at long than at short daylength (Proportion-

al hazard (Cox) regression: $\chi^2 = 68.92$, $df = 2$, $P < 0.001$ effect of light regime: $t = -7.12$, $\beta = -1.32$, $P < 0.001$; effect of number of further molts prior to adulthood: $t = 5.27$, $\beta = 0.86$, $P < 0.001$). In the case of the individuals collected as penultimate instars, the average time to their first and final molt was 41 ± 11 d ($n = 10$) and 65 ± 26.9 d ($n = 5$) under long and short daylength conditions, respectively. The minimum time to the first molt in penultimate instars was 18 d. We did not observe this type of threshold in the individuals of the three earlier stages, in which molts occurred from the first day of the experiment (Fig. 3).

In contrast to the lengths of time to first molt in the laboratory, which represent only a fragment of a complete intermolt period, the lengths of further intermolt periods, which were completely accomplished in the laboratory, did not depend significantly on either developmental status, or on light regime (Proportional hazard (Cox) regression: $\chi^2 = 3.64$, $df = 2$, $P = 0.16$ effect of light regime: $t = -0.84$, $\beta = -0.14$, $P = 0.40$; effect of number of further molts prior to adulthood: $t = -1.64$,

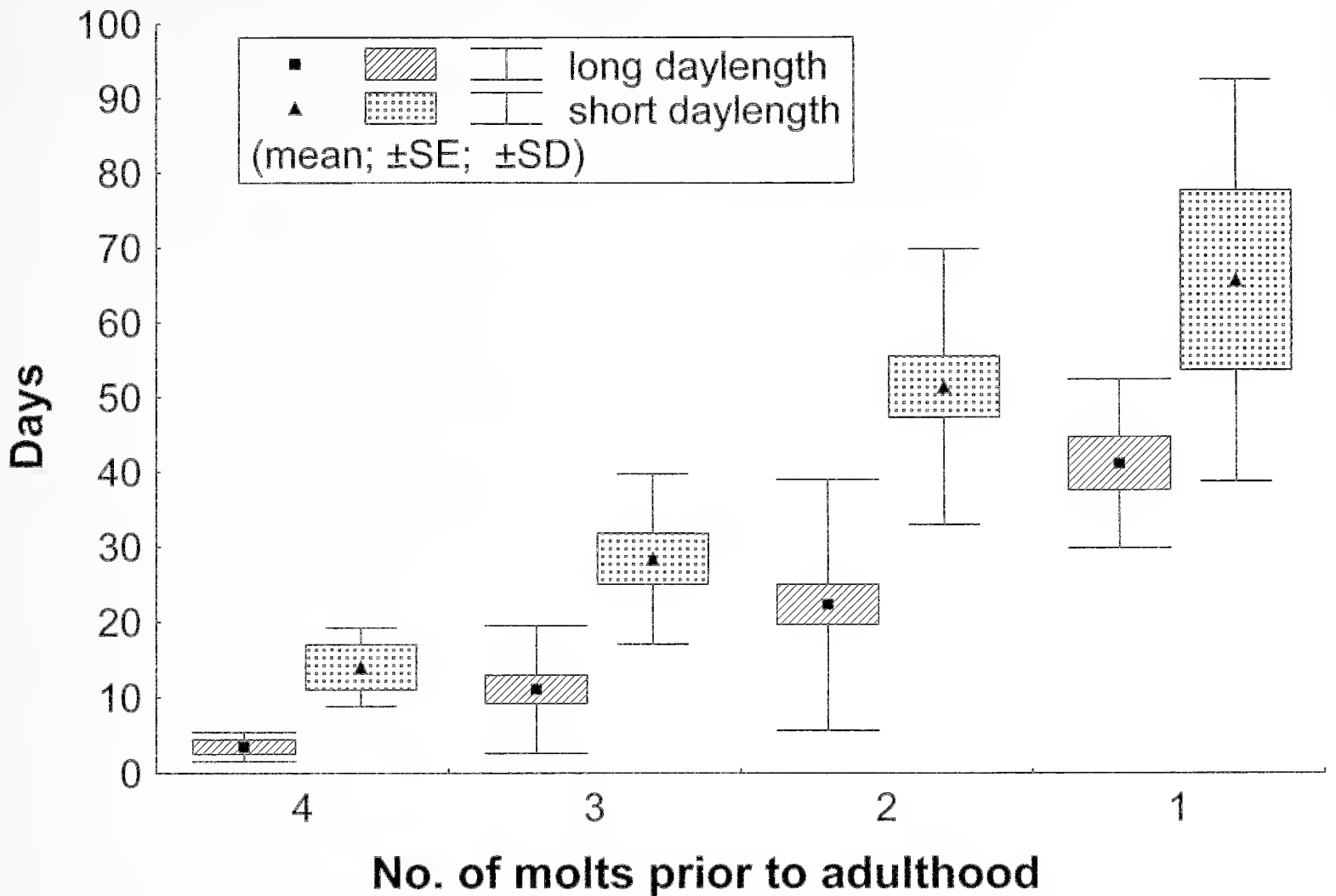


Figure 3.—Length of time to first molt from the beginning of the experiment in different developmental stages of *Pardosa agrestis* under different light regimes at indoor temperature.

$\beta = -0.28$, $P = 0.10$) (Fig. 4). Thus, differences in the time to reach adulthood were completely due to differences in the time to the first molt in the laboratory.

DISCUSSION

The results that no *Pardosa* individuals molted to adulthood at outdoor temperature, and that *P. agrestis* had a more heterogeneous stage distribution than *P. hortensis* are in accordance with our previous knowledge about the phenology of the two species (Samu et al. 1998; Samu & Szinetár in press). In contrast with the field results of Tóth et al (1997), who found that adults of *P. agrestis* males appear somewhat sooner than females in the field, under the present laboratory conditions male and female maturation times did not differ significantly from each other.

The overwhelming importance of temperature on the development rate of spiders is well known (Schaefer 1987). Our results suggest, that a clear distinction has to be made between penultimate instars and earlier juvenile stages considering the regulation of pre-overwinter-

ing development. The development of penultimate instars was halted at outdoor ambient temperatures in autumn and even the treatment of warm temperature regime with long daylength needed a considerable time to release this stasis. In contrast, the development of earlier stages of *P. agrestis* was only arrested by the relatively low autumnal outdoor temperatures and individuals in the indoor temperature groups benefited immediately from the advantageous conditions. Similar difference in the pre-overwintering development between penultimate instars and earlier juvenile stages of the same species was also reported by Schaefer (1987) in *Pirata piraticus*.

In agreement with the studies demonstrating that for a number of stenochronous species short daylength increases the lengths of the intermolt periods (Schaefer 1987), in the present study short daylength conditions decreased the tendency to molt in both species and all stages. On the other hand, short daylength was not shown to increase the number of instars in *P. agrestis*. It is rather difficult to interpret why light regime and development

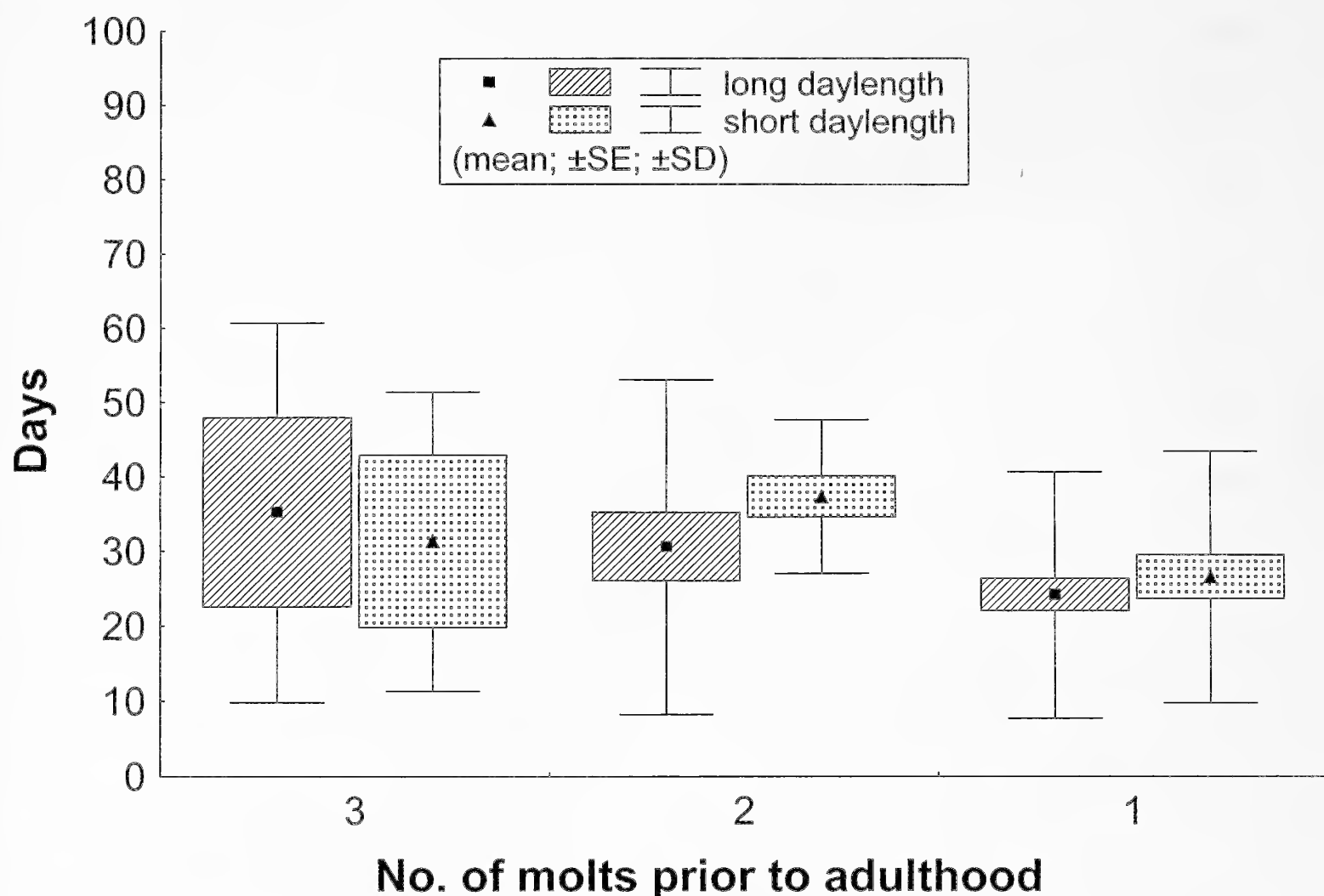


Figure 4.—Length of the intermolt periods completely accomplished in the laboratory in different developmental stages of *Pardosa agrestis* under different light regimes at indoor temperature.

stages affected only the time to the first molt in laboratory significantly, and not the further intermolt periods. We can assume that the regulation of the molting cycles and the diapause in spider species overwintering exclusively as immature instars is based on similar hormonal mechanism in different species. Bonaric (1987) found low levels of molting hormones (ecdysteroids) in the overwintering instars of *Pisaura mirabilis* (Clerck 1757) and demonstrated that the sensitivity of the overwintering instars to injected exogenous ecdysteroids increased throughout the overwintering period. This latest result can be interpreted as a possible inhibition of the effects of molting hormones at the beginning of the overwintering. Our results suggest that in *Pardosa agrestis* an inhibition of molting is increasingly present in the more developed instars in the pre-overwintering season. Once the inhibition was surmounted by artificial conditions, the molting cycles were no longer inhibited and did not depend anymore on developmental stage or light duration.

The dichotomy of the strong inhibition in autumn to reach adulthood in penultimate in-

stars, and the readiness to molt as long as favorable temperature conditions occur in earlier stages, might be a general rule in the pre-overwintering development of Holarctic stenochronous wolf spiders with spring-summer reproduction. This phenomenon certainly has a synchronizing effect on the stage composition of populations. However, this effect depends on the life history pattern of the species. In populations in which the majority of the individuals reach the penultimate stage relatively soon, individuals can compensate even considerable time-lags in their development and thus most of the individuals overwinter as penultimate instars. This is the case in *Pardosa hortensis* in Hungary in which, as a consequence, a very strict stenochrony can be observed in the appearance of adult stages at the beginning of April (Kiss pers. obs.). On the other hand, in later maturing populations in which the individuals are mostly in earlier developmental stages in autumn, the proportion of the instars reaching the penultimate stage before overwintering is highly variable year to year, depending on weather conditions. This yearly variation in the synchronization of

developmental stages in autumn may lead to different phenological patterns in different years, as it is reported for *P. agrestis* in Hungary (Samu et al. 1998).

In summary we can conclude that the pre-overwintering development of both studied species was shown to be controlled by autumnal temperature and daylength. Temperature and daylength act primarily to prevent the precocious maturation of penultimate instars. This study showed additionally that the strength of this control was stage dependent. The stronger inhibition of molting in later instars contributes differently to the stenochrony of species with different phenological pattern.

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ANNUAL DIFFERENCES AND SPECIES TURNOVER IN PEAT BOG SPIDER COMMUNITIES

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ABSTRACT. The yearly differences between material collected over two years by means of pitfall traps in three peat bogs in Lithuania and one in Finland were analyzed. Single year collections formed 58.8–87.9% of all the species collected over the two year period. No turnover occurred in the abundant species (> 1% of all specimens in one year sample) if traps were not relocated. The rates of the turnover can vary considerably in various dominance groups and show different trends at different sites. Marked annual differences in abundance were recorded even among some typically abundant peat bog species like *Pardosa sphagnicola*, *Drassyllus pusillus*, *Scotina palliardi*, *Agyneta cauta*, *Arctosa alpigena*, *Bathyphantes gracilis*, *Antistea elegans*, and *Drassodes pubescens*. Only a few species typical of other habitats were found to be permanently abundant in peat bogs. Five species recorded during the investigation are new to the spider fauna of Lithuania.

Keywords: Araneae, annual differences, communities, peat bogs, Finland, Lithuania

Evaluation of biodiversity in various invertebrate groups and habitats is a problem currently under intensive investigation. New research methods on this subject have been developed, and their effectiveness has been discussed (Duelli et al. 1990; Coddington et al. 1996; Duelli 1997; Riecken 1999, 2000). Despite known weaknesses of pitfall trapping, it is still an important sampling method used in these investigations as well as for spider research in peat bogs (Koponen 1979, 1994; Platen 1989; Schikora 1994, 1997; Relys & Dapkus 2002). Material collected during a single year is often used for inventories and bioindicator research, due to limited time and resources available for investigations. Riecken (2000) found that single year collections by pitfalls formed only 56.8%–84.0% of all species collected during a two year investigation from 20 different habitats (peat bogs not included) in Germany. Such a large number of appearing and disappearing species in a com-

munity (turnover), as well as fluctuations in relative abundance of permanently occurring species, cause annual differences in the community structure. This could result in misleading interpretations if the analyses are based on a single year. Few studies have directly addressed year-to-year differences in spider communities (Norris 1999). Two or more year's data on peat bog spiders have usually been combined in analyses (Schikora 1994; Kuprijanovitz et al. 1998). The aim of this article is to examine year-to-year differences in peat bog spider communities. We also try to identify and discuss the most stable species groups, suitable for use as indicators in peat bogs.

METHODS

Study sites.—This research was carried out in three peat bogs (L-A, L-B, L-C) in Eastern Lithuania: Balosa (L-A, 54°53'N, 25°48'E), Kertusas (L-B, 55°08'N, 24°54'E), Laukenai (L-C, 55°11'N, 25°03'E), and in one peat bog in Southern Finland: Kareva (F, 60°32'N, 22°09'E). The peat bogs in Lithuania were pine bogs (*Pinus silvestris*–*Ledum palustre*–

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Sphagnum) overgrown with pine trees of various age and density. The bog in Finland was an open peat bog (*Eriophorum vaginatum*–*Sphagnum*).

Data collection.—All collecting was done with pitfall traps. The data in Lithuania were collected in 1999 and 2000. Data from Finland were collected in 1964 and 1966 and used to provide information about the differences between the samples separated by one year (1965). Six plastic jars (volume 300 ml, depth 10 cm, diameter 7 cm) filled with 100–120 ml of 4% formaldehyde solution mixed with drops of detergent were used at each locality in Lithuania. In Lithuania the traps were operated from April–October in 1999 and 2000. The traps were emptied every 3 weeks. In Finland 20 traps with ethylene glycol and detergent were set 1.5–2 m apart and emptied in 2 week intervals, June–August 1964 and 1966. The traps in one peat bog in Lithuania (L-C) were moved in 2000 about 90 m from the site investigated in 1999. There were no marked differences in vegetation between the sites. The abbreviations of samples taken from Lithuania in 1999 are L-A99, L-B99, and L-C99, and samples taken in 2000 are L-A00, L-B00, and L-C00. F64 and F66 refer to the years of studies performed in Finland in 1964 and 1966.

Data analysis.—Turnover index: The rates of turnover in a community between time periods are of a qualitative nature and can be described as the index of turnover. According to MacArthur & Wilson (1967), turnover estimates the number of local colonizations and extinctions related to the number of species in the community. Originally this index was developed for islands; it can also be used for isolated terrestrial units often called “terrestrial islands”. Peat bogs, especially small ones surrounded by other habitat types and bearing unique or stenotopic elements of flora and fauna, often represent typical cases of such “islands”. The use of the turnover index for spider communities was demonstrated by Norris (1999). The turnover index (T_n) was calculated by dividing the sum of appearing and disappearing species over two years by the sum of species found in each of the years (Russell et al. 1995; Norris 1999). The index ranges from 0–1. *Percent similarity coefficient*: We use this abundance-based coefficient (PSc) to describe changes in species abundance in

whole sets of species and in various dominance (abundance) groups in communities between the years. The coefficient reflects similarity of proportional representation of the species in the community and is not affected by the sample size. Higher coefficient values indicate higher similarity and show lower differences and changes in species abundance. The formula for calculating PSc can be obtained from Wolda (1981). Like some other abundance-based measures, the percent similarity coefficient, being of quantitative nature, is also affected by turnover, especially if it occurs in abundant species.

Nomenclature used is according to Platnick (1997) and the material from Lithuania and Finland is deposited in the Zoological Museum of the Department of Zoology, Vilnius University and in the Zoological Museum, University of Turku, respectively.

RESULTS AND DISCUSSION

General overview of the data.—The material analyzed comprised 8245 adult spider specimens representing 146 species. Of these, 43 species were singletons, and another 32 were represented by three or fewer specimens. The differences in species and individual numbers were obvious in all communities for the compared years (Table 1). In L-B and L-C, higher species diversity was registered in the year with fewer individuals. More than 50% of all species found each year were represented by three or fewer individuals. An increase in the total number of species due to newly appearing species was found in all the communities during the second year of the study. The percentage of species found during a single study year (58.8–87.9% of the total two-year collection) was very close to that (average 74.5%) found in 20 different habitats by Riecken (2000), using the same collecting methods. On average, 75.2% of species were found by us during a single year in the peat bogs. Only a few species were consistently found in low numbers. Even some of small-sized species of Linyphiidae or Theridiidae (*Agyneta* spp., *Bathyphantes* spp., *Bolyphantes* spp., *Maro* spp., *Theonoe minutissima* (O.P.-Cambridge 1879), etc.) were found in high numbers in some years. This shows that the data obtained by pitfall trapping could also provide valuable information about the relative abundance of such species. Five species

Table 1.—Data on the spider material collected during two years from four peat bogs in Lithuania and Finland. L-A = Balosa, L-B = Kertusas, L-C = Laukenai, = Kareva. Samples taken in 1999 are L-A99, L-B99, L-C99 and in 2000: L-A00, L-B00, and L-C00. F64 and F66 refer to the years of studies performed in Finland in 1964 and 1966.

	L-A99	L-A00	L-B99	L-B00	L-C99	L-C00	F-64	F-66
No. individuals	765	752	1202	907	1147	852	1455	1165
No. species/year	52	48	47	62	40	51	73	55
No. species/total (two years)		60		74		68		83
Appeared/Disappeared in second year		8/12		27/12		28/17		9/26
% of species of two years in one year	86.6	80	63.5	83.8	58.8	75	87.9	66.3
No. species < 3 individuals	33	25	24	37	21	30	42	28
% species < 3 individuals	63.5	52.1	51.1	59.7	52.5	58.8	57.5	50.9
No. species > 3 individuals	19	23	23	25	19	21	31	27
No. species (> 1% of indiv.) in one year	9	14	13	15	12	13	15	11
% species (>1% of indiv.) in one year	17.3	29.2	27.7	24.2	30.0	25.5	20.5	20.0

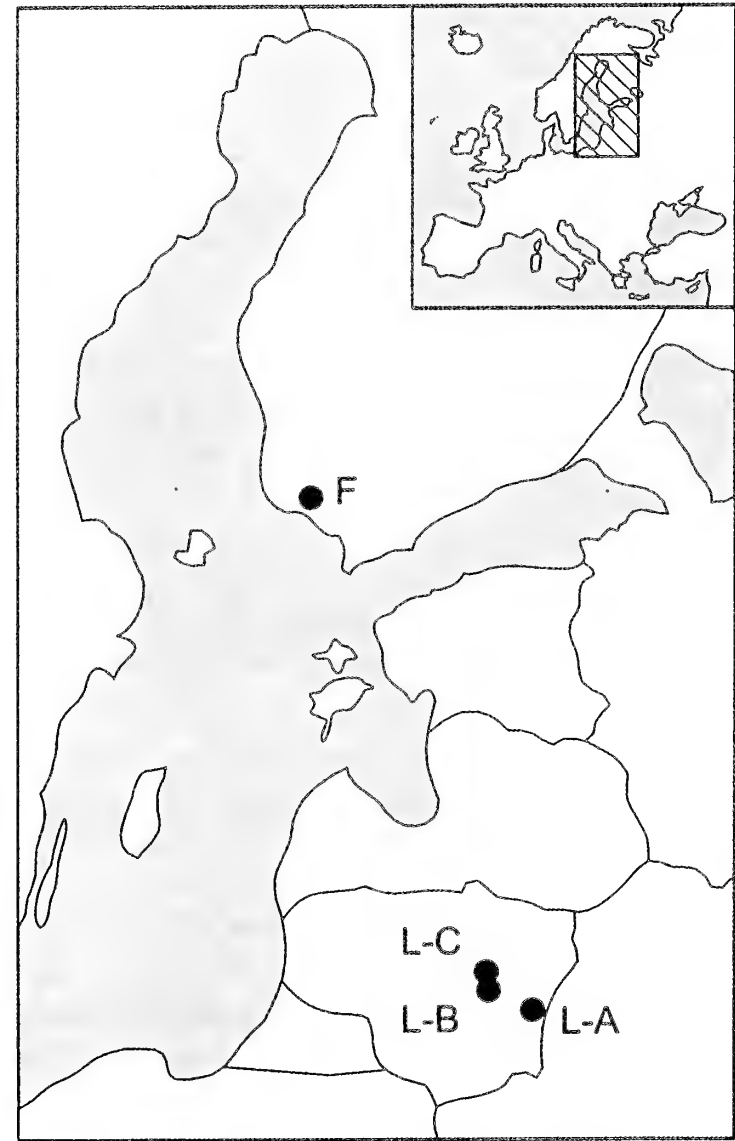


Figure 1.—Study sites in northern Europe: L-A = Balosa, L-B = Kertusas, and L-C = Laukenai (Lithuania), F = Kareva (Finland).

found during the investigation are newly reported for Lithuanian. These are: *Robertus lyrifer* Holm 1939, *Theridium mystaceum* L. Koch 1870 (both Theridiidae), *Diplocephalus dentatus* Tullgren 1955 (Linyphiidae), *Acantholycosa lignaria* (Clerck 1757) (Lycosidae) and *Xysticus lineatus* (Westring 1851) (Thomisidae). The list of species and numbers of individuals found in the peat bogs investigated in Lithuania are given in the Table 4.

Yearly turnover.—The turnover of species shows various trends when the whole data set is analyzed (Table 1). More species appeared from L-B and L-C, and disappeared in F. A situation close to equilibrium was recorded from L-A. Up to 52.7% of the species found during two years at the same place were only residents for a single year. The high proportion of species occurring in a single year from L-C (66.2%) was probably due to the relocation of the traps, where besides temporal turnover, there was also spatial turnover (Russell 1999). The case of L-A showed that low rates of turnover can be observed at the same place ($T_n = 0.1$), while the internal changes between the abundance groups remained well expressed (Table 2). On the other hand, the case of L-B showed that high rates of the turnover could also exist at the same place ($T_n = 0.36$).

The highest turnover rates were found in the group of species with three or fewer specimens. In the case of L-B, the high turnover

Table 2.—Turnover index (Tn) and percent similarity coefficient (PSc) in various dominance groups of peat bog spider communities in Lithuania and Finland. Localities as in Table 1. Asterisk (*) indicates the groups of species where no turnover occurred.

	Turnover index (Tn)				Percent similarity (PSc)			
	L-A	L-B	L-C	F	L-A	L-B	L-C	F
Whole set of species	0.1	0.36	0.49	0.3	67.5	62.3	49.7	59.5
Species with >3 individuals	0.09	0.1	0.25	0.09	68.1	63.0	50.4	59.7
Species with <3 individuals	0.36	0.79	0.81	0.65	56.0	32.9	11.9	45.4
Species with >1% of dominance	*	*	0.15	*	69.2	62.0	54.1	61.5
10 most abundant species	*	*	0.17	*	69.2	62.3	49.7	61.2

rate ($Tn = 0.79$) in this group of species influenced the high turnover rate of the entire data set ($Tn = 0.36$). The turnover rate for the rest of the community (> 3 individuals) was similar in all communities where no traps were relocated ($Tn = 0.09$ – 0.1). No turnover was found in the group of species representing more as 1% of the individuals, if the traps were not moved. Thus, the changes in this group of species were only due to increasing or decreasing abundance of species permanently occurring in the community.

Differences in abundance.—Other differences appearing in the communities between years are due to the changing abundance of species. This is the main cause of the observed differences in the groups of higher dominance in which no turnover occurred. It was clearly seen that the highest changes resulting in the lowest similarity values (PSc) in all selected groups were registered in peat bog L-C, where the traps were moved the following year (Table 2). The smallest changes ($PSc = 67.5$) were recorded in peat bog L-A, where moderate variation in the abundance in the most abundant species was observed. The

higher differences in abundance of some dominate species, e.g., *Pardosa sphagnicola* (Dahl 1908), *Scotina palliardi* (L. Koch 1881), were found in peat bog L-B, and contributed to the lower similarity ($PSc = 62.3$) in this peat bog. The situation in Finnish peat bogs ($PSc = 59.5$) was similar to that observed from L-B. Higher differences as compared to the Lithuanian material could be caused by the additional year between samples.

Additionally we looked for the most stable group of species occurring at the same dominance level during both years. We found that there was a stable set of species (15–18) reaching more than 1% of dominance in one of the years. Only a few (2–3) species left this group and became less abundant in one of the years. In peat bog L-B there was only one such species. It is important to notice that no turnover was found in this dominance group if the traps remained in the same place.

A number of species remained abundant in all communities during both years of the study (Table 3), despite the changed sites in peat bog (L-C) or the geographical location of the site (cf. also Koponen et al. 2001). These spe-

Table 3.—Relative abundance (%) of the most abundant spider species consistently occurring in peat bogs in Lithuania and Finland. Localities as in Table 1.

	L-A99	L-A00	L-B99	L-B00	L-C99	L-C00	F-64	F-66
<i>Pirata uliginosus</i>	5.88	9.84	6.66	3.86	14.82	27.93	39.93	23.18
<i>Trochosa spinipalpis</i>	4.44	12.50	4.41	7.83	2.35	3.40	3.37	4.29
<i>Lepthyphantes angulatus</i>	4.96	3.06	2.08	1.98	0.87	0.82	2.61	1.03
<i>Pardosa sphagnicola</i>	9.15	9.04	27.96	1.54	23.10	1.88	3.02	2.15
<i>Scotina palliardi</i>	0.52	5.19	3.16	17.42	14.30	10.92	0.14	0.52
<i>Centromerus arcanus</i>	2.22	1.20	2.41	1.43	1.22	1.17	0.14	
<i>Aulonia albirana</i>	47.06	27.79	23.88	32.75	25.72	15.26		
<i>Hygrolycosa rubrofasciata</i>	5.09	9.44	3.16	1.76	0.17	2.58		

Table 4.—Species and numbers of spiders in peat bog communities studied in Lithuania in 1999 and 2000. Localities as in Table 1.

Localities	L-A99	L-A00	L-B99	L-B00	L-C99	L-C00
<i>Crustulina guttata</i> (Wider)						1
<i>Dipoena prona</i> (Menge)		1		2		
<i>Euryopis flavomaculata</i> (C. L. Koch)		1				2
<i>Robertus arundineti</i> (O.P.-Cambr.)						2
<i>Robertus lividus</i> (Blkw.)			1	2		
<i>Robertus lyrifer</i> Holm				1		
<i>Theonoe minutissima</i> (O.P.-Cambr.)	1	7	1	9		4
<i>Theridion mystaceum</i> L. Koch			1			
<i>Agyneta cauta</i> (O.P.-Cambr.)	3	23	142	46	1	95
<i>Agyneta conigera</i> (O.P.-Cambr.)				6		1
<i>Agyneta decora</i> (O.P.-Cambr.)						1
<i>Bathyphanes gracilis</i> (Blkw.)					3	
<i>Centromerus aequalis</i> (Westring)	1			1		
<i>Centromerus arcanus</i> (O.P.-Cambr.)	17	9	29	13	14	10
<i>Centromerus levitarsis</i> (Simon)	3	2			13	
<i>Centromerus sylvaticus</i> (Blkw.)			4	1	4	
<i>Ceratinella brevis</i> (Wider)			2	3	1	2
<i>Cnephalocotes obscurus</i> (Blkw.)	1	1	3	4	15	
<i>Diplocephalus dentatus</i> Tullgren						1
<i>Dismodicus elevatus</i> (C. L. Koch)				1		
<i>Gonatium rubens</i> (Blkw.)	3	7	3	1		
<i>Gongylidiellum murcidum</i> Simon	1					
<i>Lepthyphantes angulatus</i> (O.P.-Cambr.)	38	23	25	18	10	7
<i>Lepthyphantes cristatus</i> (Menge)	1		6	2		3
<i>Lepthyphantes mengei</i> Kulcz.		4		1	3	
<i>Linyphia trianguaris</i> (Clerck)	1					
<i>Lophomma punctatum</i> (Blkw.)				1		
<i>Macrargus carpenteri</i> (O.P.-Cambr.)				2		2
<i>Maro minutus</i> O.P.-Cambr.				7	2	23
<i>Meioneta affinis</i> (Kulcz.)						2
<i>Meioneta mossica</i> Schikora					1	
<i>Micrargus apertus</i> (O.P.-Cambr.)			4	3	1	
<i>Microneta viaria</i> (Blkw.)				2		
<i>Neriere radiata</i> (Walck.)	1	1				
<i>Pocadicnemis pumila</i> (Blkw.)	1	10	22	41	1	13
<i>Savignia frontata</i> Blkw.						1
<i>Sintula corniger</i> (Blkw.)			5	2	5	2
<i>Stemonyphantes lineatus</i> (Linnaeus)			1		2	
<i>Tallusia experta</i> (O.P.-Cambr.)	9	6	2	1	13	
<i>Tapinocyba insecta</i> (L. Koch)				1		
<i>Tapinocyba pallens</i> (O.P.-Cambr.)					1	
<i>Taranucnus setosus</i> (O.P.-Cambr.)	1	1		1	2	
<i>Walckenaeria alticeps</i> (Denis)	2	10	15	24		6
<i>Walckenaeria atrotibialis</i> O.P.-Cambr.	4	6	11	7	1	6

Table 4.—Continued.

Localities	L-A99	L-A00	L-B99	L-B00	L-C99	L-C00
<i>Walckenaeria cuspidata</i> Blkw.	1			1	1	
<i>Walckenaeria karpinskii</i> (O.P.- Cambr.)		1				
<i>Walckenaeria nodosa</i> O.P.- Cambr.				1	9	
<i>Walckenaeria nudipalpis</i> (Westr- ing)	2	1	2	3		1
<i>Pachygnatha clercki</i> Sundevall					1	1
<i>Pachygnatha degeeri</i> Sundevall	1		1	2	7	1
<i>Pachygnatha listeri</i> Sundevall						2
<i>Cercidia prominens</i> (Westring)	4		4			2
<i>Hyposinga sanguinea</i> (C. L. Koch)						1
<i>Acantholycosa lignaria</i> (Clerck)			1			
<i>Alopecosa pulverulenta</i> (Clerck)	53	12				
<i>Arctosa alpigena</i> (Doleschall)			5		15	2
<i>Aulonia albimana</i> (Walck.)	360	209	287	297	295	130
<i>Hygrolycosa rubrofasciata</i> (Ohl- ert)	39	71	38	16	2	22
<i>Pardosa lugubris</i> (Walck.)				1		
<i>Pardosa prativaga</i> (L. Koch)	4	7		1		3
<i>Pardosa pullata</i> (Clerck)	2	3		1	11	66
<i>Pardosa sphagnicola</i> (Dahl)	70	68	264	14	265	16
<i>Pirata hygrophilus</i> Thorell			3	5		
<i>Pirata insularis</i> Emerton			2	5		
<i>Pirata piraticus</i> (Clerck)			1			
<i>Pirata ulginosus</i> (Thorell)	45	74	80	35	170	238
<i>Trochosa ruricola</i> (De Geer)	2	2				
<i>Trochosa spinipalpis</i> (F.O.P.- Cambr.)	34	94	53	71	27	29
<i>Dolomedes fimbriatus</i> (Clerck)	2			1		
<i>Antistea elegans</i> (Blkw.)	3	3	3	1	32	
<i>Hahnia pusilla</i> C. L. Koch	1	2	4	7		13
<i>Cicurina cicur</i> (Fabricius)			2			
<i>Agroeca brunnea</i> (Blkw.)	1	4				
<i>Agroeca dentigera</i> Kulcz.	7	11		1	3	7
<i>Aroeca proxima</i> (O.P.-Cambr.)	1	2		1		2
<i>Phrurolithus festivus</i> (C. L. Koch)		4	2	3		
<i>Phrurolithus minimus</i> C. L. Koch	2					
<i>Scotina palliardi</i> (L. Koch)	4	39	38	158	164	93
<i>Clubiona diversa</i> O.P.-Cambr.					1	
<i>Drassodes pubescens</i> (Thorell)	1		1			
<i>Drassyllus lutetianus</i> (L. Koch)	4	2	2	2		2
<i>Drassyllus pusillus</i> (C. L. Koch)	5	3	64	11	41	10
<i>Gnaphosa microps</i> Holm	5	9	46	33	2	
<i>Gnaphosa nigerrima</i> L. Koch	4	2			2	
<i>Haplodrassus moderatus</i> (Kulcz.)		3	1			
<i>Haplodrassus signifer</i> (C. L. Koch)	3	1	2	6	4	4
<i>Haplodrassus silvestris</i> (Blkw.)	1					
<i>Haplodrassus soerenseni</i> (Strand)						1
<i>Micaria pulicaria</i> (Sundevall)				3		

Table 4.—Continued.

Localities	L-A99	L-A00	L-B99	L-B00	L-C99	L-C00
<i>Zelotes clivicola</i> (L. Koch)				1		
<i>Zelotes latreillei</i> (Simon)	2	1	3		1	1
<i>Zelotes longipes</i> (L. Koch)						1
<i>Zelotes subterraneus</i> (C. L. Koch)	1					
<i>Zora silvestris</i> Kulcz.		1	9	9	1	1
<i>Zora spinimana</i> (Sundevall)	7	4	1			
<i>Xysticus cristatus</i> (Clerck)	1	1		1		1
<i>Xysticus lineatus</i> (Westring)						4
<i>Xysticus ulmi</i> (Hann)		1				
<i>Euophrys frontalis</i> (Walck.)				1		
<i>Euophrys westringi</i> (Simon)	1	3		2		3
<i>Evarcha arcuata</i> (Clerck)	2	1				
<i>Evarcha falcata</i> (Clerck)				5		
<i>Evarcha laetabunda</i> (C. L. Koch)						2
<i>Heliophanus dubius</i> C. L. Koch				1		
<i>Neon reticulatus</i> (Blkw.)	2	1	5	4		8
<i>Neon valentulus</i> Falconer						1
<i>Talavera petrensis</i> C. L. Koch			1			
Spider totals	765	752	1202	907	1147	852
Species totals each year	52	48	47	62	40	51
Species totals in two years		60		74		68

cies are the most stable components of epigeic peat bog spider communities in the entire investigated region. Absence or lower than typical abundance of such species can probably indicate disturbance of the peat bog habitat. *Pirata uliginosus* (Thorell 1856), *Centromerus arcanus* (O.P.-Cambridge 1873) and *Lepthyphantes angulatus* (O.P.-Cambridge 1881) showed the lowest differences in abundance between the two years. On the other hand, some large differences in the abundance of some typical peat bog species were found between the studied years. *Pardosa sphagnicola* showed differences in one locality (L-B) similar to those observed in the case of the changed site (L-C), but the dominance of this species always exceeded 1%. Marked differences in abundance have been recorded for *Aulonia albirana* (Walckenaer 1805) occurring only in Lithuania, but this species was always dominant in the communities investigated (Table 3). *Trochosa spinipalpis* (F.O.P.-Cambridge 1859) from L-A and *Scotina pallardi* from L-A and L-B showed much larger differences in abundance at the same locality as compared to the differences found when the traps were moved (Table 3). Such fluctuations in the abundance of even typical peat bog spe-

cies could lead to erroneous interpretations of the data about respective species living in peat bogs and should be considered if studies are restricted to one year.

The data show that most of the species found in both years were mainly hygrophilous or typical peat bog species. Only a few species that are common in other habitats were often abundant (> 1%) in any of the studied peat bogs during both years: *Alopecosa pulverulenta* (Clerck 1757) at L-A and F, *Agyneta cauta* (O.P.-Cambridge 1902) at L-B and F, *Pardosa prativaga* (L. Koch 1870) at L-A, *Pardosa pullata* (Clerck 1757) in F, *Drassylus pusillus* (C. L. Koch 1833) and *Walckenaeria alticeps* (Denis 1952) at L-B.

Effect of repositioning.—The data obtained from peat bog L-C, where the traps were moved in the second year, showed considerable differences compared to the other communities. This repositioning resulted in a higher turnover and a lower similarity in all abundance groups in comparison to the other peat bogs (Table 2). The turnover (five species, $T_n = 0.15$) occurred even in the species with high abundance (> 1%), which was not the case in the other peat bogs. The relocation of traps did not markedly affect the total num-

ber of species collected. The number remained lower (68 species) than L-B (74). The lowest number of permanently found species, recorded as three or fewer specimens (4 species), was recorded in this peat bog, while 15 and 14 such species were found at L-A and F respectively. The highest difference in abundant species was found at L-C as well. From species with more than 3 individuals, 28% occurred during a single year of study at L-C, while only 11.1% and 8.3% occurred for a single year at L-A and L-B, respectively. Not all the differences found at L-C could be explained by temporal turnover or by the changes in abundance observed in other peat bogs. As it was already mentioned, the spatial turnover was an additional case here and contributed to the higher differences (Russell 1999). Thus, an aggregated distribution of spiders and heterogeneity of their communities in peat bogs could be supposed despite similar vegetation.

Data from Finland.—Despite slightly different methods, geographical location and time of research, the Finland data showed similar trends to communities studied in Lithuania. Geographically defined differences between peat bog spider communities have been analyzed (Koponen et al. 2001). Most of the abundant ($> 0.5\%$) species registered in Finland, with exception of those known only for Finland, were also abundant in Lithuanian peat bogs during one or both years (Table 3). Lower similarity between the samples could be the result of the one year interval between collections in Finland. The turnover ($T_n = 0.3$) was the same as that observed in Lithuania (Table 2).

CONCLUSIONS

Peat bogs are stable and slowly changing habitats if natural conditions are preserved (Masing 1984; Succow 2000). However, in the case of spider faunas, studied by the means of pitfall traps, high variation in species composition and abundance occurred between years in peat bogs. Even some typical peat bog species show considerable differences in their abundance. Hence, the occurrence of large fluctuations should be taken into account in inventories of fauna and in studies using indicator species in peat bogs. It could be suggested that the 15 most abundant species be used to get the main representative set of spe-

cies if study is restricted to a single year. The species in this set do not undergo turnover and they remain abundant during two consecutive years in peat bogs investigated in Lithuania. This set, consisting mainly of hygrophilous or typical peat bog species, can be easily defined and used as a diagnostic tool for the natural state of peat bog habitats. We assume that the growing number and permanent abundant occurrence of eurytopic species or species especially typical of other habitats may indicate changes in living conditions in a peat bog.

The part of the species in the groups showing the highest turnover may be species entering communities passively by ballooning. These species (sometimes in high numbers) land in inappropriate habitats and live there only temporarily, causing turnover. Marked differences in spider communities were revealed if traps were relocated in the same peat bog. Communities were also influenced by additional spatial turnover. The results clearly follow statement of Russell (1999), that “the greater the separation in time or space, the greater the difference in species composition”. This statement is supported also by data from Finland, showing higher differences between samples separated by a single year in comparison to the samples from two consecutive years in Lithuania.

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PENIS MORPHOLOGY IN ONCOPODIDAE (OPILIONES, LANIATORES): EVOLUTIONARY TRENDS AND RELATIONSHIPS

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ABSTRACT. An interim report on our ongoing revisional study is given together with a short summary of the current knowledge on the systematics and distribution of the family Oncopodidae (Opiliones, Laniatores). An exceptionally high diversity in male genitalia is shown and its possible evolution is discussed. Four major penis types are distinguished in the Oncopodidae and compared with similar forms in other laniatorean families.

Keywords: Opiliones, Oncopodidae, penis types, Asia

The Oncopodidae is a family of obscure, soil-dwelling opilionids, which are easily recognizable by a general lack of spines and tubercles (which are otherwise typical for Laniatores), by a simple palp with a small claw, by fairly short, stout legs with few (1–3) tarsalia, and by a very large dorsal and ventral scutum (scutum completum), which leaves only the anal plate (tergite IX) free. These characters are probably plesiomorphic. Apomorphic traits defining the Oncopodidae as a monophyletic group are rather sparse. The most obvious one is a carapace-abdomen bridge formed by paired or unpaired cuticular processes on the posterior margin of the prosomal and on the anterior margin of the opisthosomal part of the dorsal scutum. The other apomorphies are less conspicuous, i.e. glans penis with paired lateral sclerites connected by an intermediate plate; ovipositor short and laterally compressed. Oncopodids were previously regarded as extremely rare, poor in species diversity, and morphologically uniform (Šilhavý 1961; Martens 1977, 1986). In the course of our taxonomic revision of this

family (Martens & Schwendinger 1998; Schwendinger & Martens 1999, 2002) several new taxa were described, but the truly remarkable discovery of this study is the surprisingly high diversity of penis forms present. This richness in genital morphology in described and yet undescribed species is shown and compared with similar penis forms in other opilionid families in the following provisional summary of our results.

METHODS

The methods applied were described in Schwendinger & Martens (2002). Abbreviations used in the text are as follows: MAR = collection of J. Martens, Mainz ; MHNG = Muséum d'histoire naturelle, Genève; MSNG = Museo Civico di Storia Naturale, Genova.

SYSTEMATICS

Family Oncopodidae Thorell 1876

Type genus: *Oncopus* Thorell 1876 by monotypy.

Genus *Oncopus* Thorell 1876

Type species.—*Oncopus doriae* Thorell 1876 by original designation (1 female and 1 juvenile syntype deposited in MSNG).

Species account and distribution.—Seven species; known from Thailand (doubtful record), peninsular Malaysia, Singapore, Sarawak and Sabah.

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Main characteristics.—Glans penis proximad-directed (Figs. 1–4); tarsal formula 1-1-1-1; body large; chelicerae massive, with ventral process on 2nd (sometimes also on 3rd) article; ventroproximal process on palpal tibia distinct; ventral process on palpal trochanter slightly distad-inclined.

Genus *Gnomulus* Thorell 1890

Type species.—*Gnomulus sumatranus* Thorell 1891 by ruling of the International Commission on Zoological Nomenclature (2001) (male lectotype, 3 female and 2 juvenile paralectotypes deposited in MSNG).

Species account and distribution.—48 species; known from the Himalayan region (central and east Nepal, NE-India), southern China, and from all over SE-Asia, as far east as Waigeo Island off the northwestern tip of New Guinea.

Main characteristics.—Glans penis proximad-directed, with a tendency for reduction and modification of different elements of the glans (Figs. 5–22); tarsal formula 2–2–3(2)–3(2); body small to large; chelicerae weak to massive, without ventral processes on 2nd and 3rd article; ventroproximal process on palpal tibia absent or developed as a low, rounded hump (distinct only in *G. sumatranus*); ventral process on palpal trochanter ventrad-directed, distad-directed or absent.

Genus *Caenoncopus* Martens & Schwendinger 1998

Type species.—*Oncopus cuspidatus* Schwendinger 1992 by original designation (male holotype and male paratype deposited in MHNG).

Species account and distribution.—Three species from Sumatra.

Main characteristics.—Glans penis hypertrophied, asymmetrical, proximad-directed (Figs. 23–28); tarsal formula 1–1–3(2)–3(2); body small; chelicerae weak, without processes on 2nd and 3rd article; no ventral process on palpal tibia; ventral process on palpal trochanter ventrad-directed.

Genus *Palaeoncopus* Martens & Schwendinger 1998

Type species.—*Palaeoncopus gunung* Martens & Schwendinger 1998 by original designation (male holotype and 3 female para-

types deposited in MHNG, 1 male and 1 female paratypes in MAR).

Species account and distribution.—Three species from Sumatra.

Main characteristics.—Glans penis distad-directed, not expandible; membranous tubes of glans reduced or absent (Figs. 31–35); tarsal formula 1-1-3-3; palpal trochanter with prodorsal cone; body small; chelicerae weak, without processes on 2nd and 3rd article; no ventral process on palpal tibia; ventral process on palpal trochanter distad-directed.

Genus *Biantoncopus* Martens & Schwendinger 1998

Type species.—*Biantoncopus fuscus* Martens & Schwendinger 1998 by original designation and monotypy (male holotype, 2 male and 3 female paratypes deposited in MHNG, 1 male and 1 female paratypes in MAR).

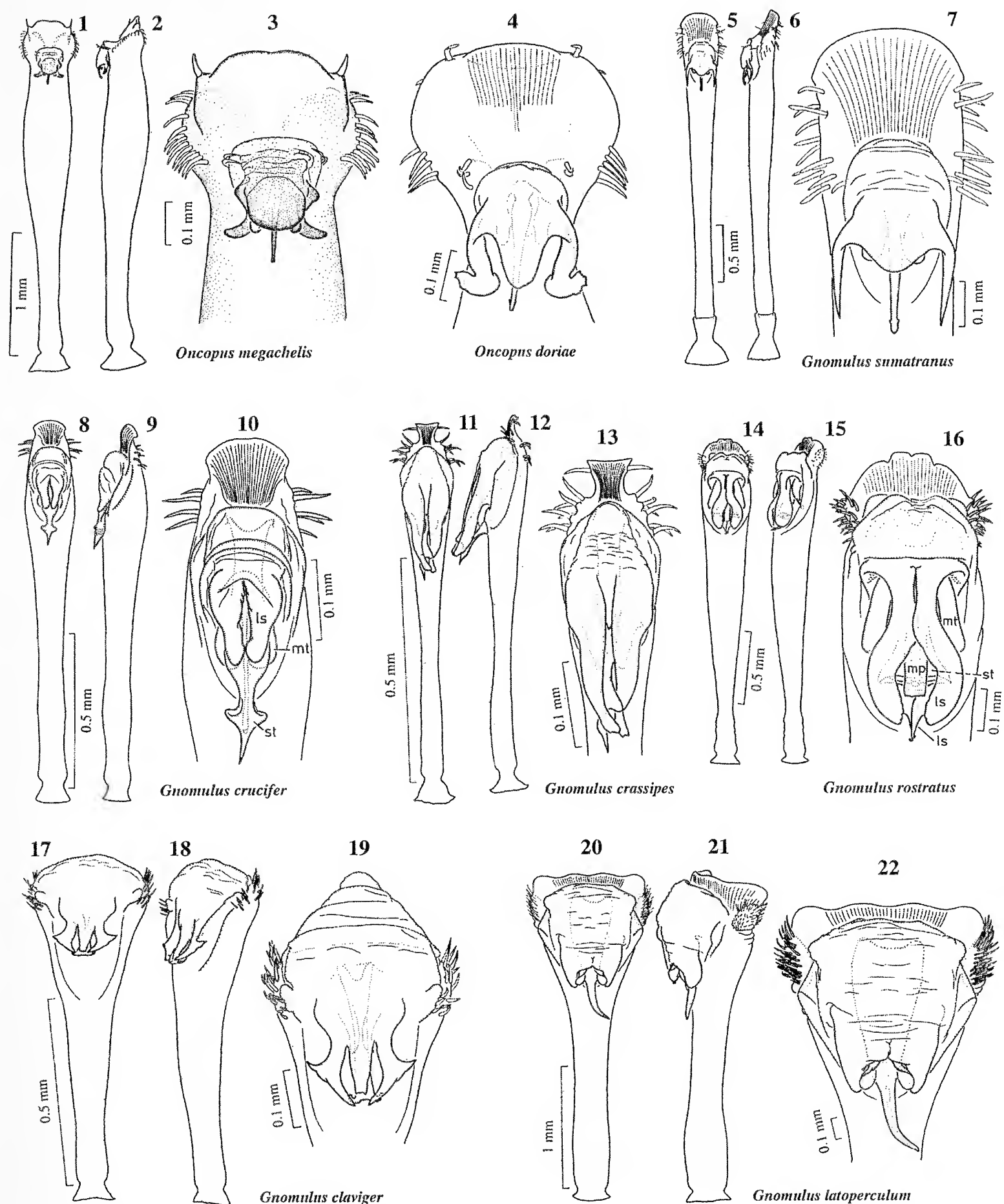
Species account and distribution.—One species from Leyte Island, the Philippines.

Main characteristics.—Glans penis distad-directed, expandible (Figs. 39–46); tarsal formula 2-2-3-3; body small; chelicerae weak, without processes on 2nd and 3rd article; no ventral process on palpal tibia; ventral process on palpal trochanter distad-directed.

PENIS MORPHOLOGY

The oncopodid penis is of the hemolymph-pressure type, i.e. the truncus penis lacks muscles and the complex of glans sclerites (Figs. 55–56) is agitated by internal pressure. The shape of the subterminal glans is highly species-specific (with considerable interspecific variation in the genus *Gnomulus*; see Figs. 5–22) and its orientation and functional morphology allow us to draw generic boundaries in most cases (except between *Oncopus* and *Gnomulus*). Four major penis types can be distinguished (see also Martens & Schwendinger 1998):

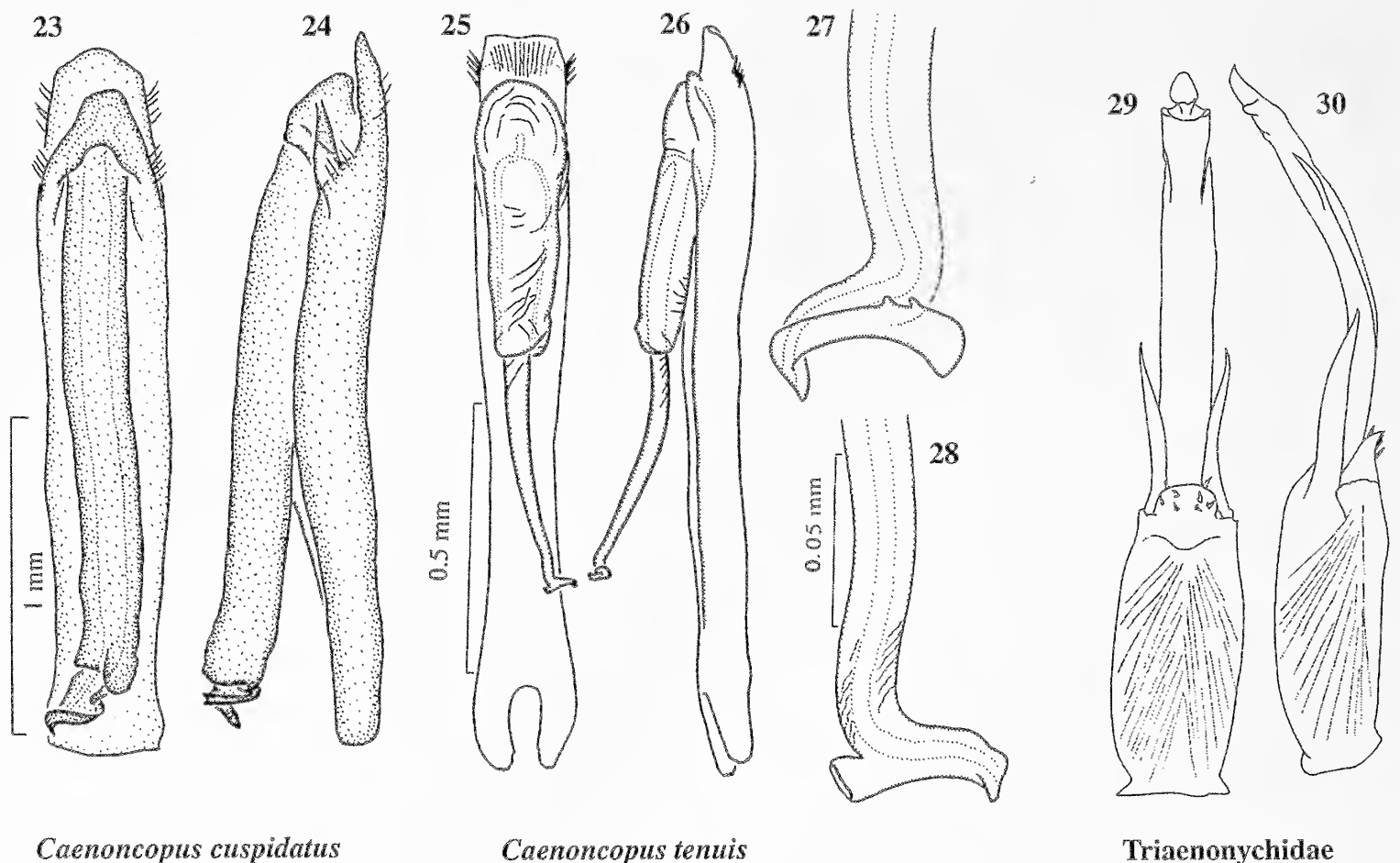
Type 1.—*Palaeoncopus* species possess a slender penis with a short, distad-directed glans (Figs. 31–35). Expansion of the glans in hot lactic acid causes the glans to spread away only slightly from the truncus without protruding the stylus (Fig. 34). Penes with a distad-directed glans are found in most laniato-rean opilionids and therefore this type is probably plesiomorphic. A quite similar glans structure was illustrated for the phalangodid



Figures 1–22.—Penis type 3: 1–3. *Oncopus megachelis* Schwendinger; 4. *O. doriae* Thorell; 5–7. *Gnomulus sumatranus*; 8–10. *G. crucifer* Martens & Schwendinger; 11–13. *G. crassipes* Schwendinger & Martens; 14–16. *G. rostratus* Thorell; 17–19. *G. claviger* Schwendinger & Martens; 20–22. *G. latoperculum* Schwendinger & Martens. 1, 5, 8, 11, 14, 17, 20. Total penis, dorsal view; 2, 6, 9, 12, 15, 18, 21. Total penis, lateral view; 3, 4, 7, 10, 13, 16, 19, 22. Apex of penis, dorsal view.

Haasus judaeus Roewer 1949 (Figs. 37–38; see Martens 1976). The described species of *Palaeoncopus* all lack paired membranous tubes in their glans penis (Fig. 33), which is

certainly an apomorphic reduction, but an undescribed species from a cave on Sumatra still possesses a small pair of these tubes (Fig. 35). As the absence of this glans element was be-

*Caenoncopus cuspidatus**Caenoncopus tenuis*

Triaenonychidae

Figures 23–30.—23–28. Penis type 4: 23–24. *Caenoncopus cuspidatus*; 25–28. *C. tenuis* Martens & Schwendinger; 29, 30. *Cluniella minuta* Forster (Triaenonychidae) (from Hunt & Maury 1993). 23, 25, 29. Total penis, dorsal view; 24, 26, 30. Total penis, lateral view; 27, 28. Tip of stylus, different positions.

fore considered characteristic for *Palaeoncopus*, its diagnosis has to be changed.

A distad-directed, non-expandible glans with small membranous tubes was unexpectedly also found in an undescribed species from Nepal (Fig. 36), but we doubt if it is closely related to *Palaeoncopus*. Its stouter penis, different tarsal formula (2-2-3-3 instead of 1-1-3-3), larger body, and palpal trochanter with ventrad-directed ventral process but without prodorsal cone, rather indicate that the Nepalese species is a *Gnomulus* with reversal in its glans orientation.

Type 2.—The penis of *Biantoncopus fuscus* (Figs. 39–44) also has a distad-directed glans, but its structure is distinctly more complicated and—more importantly—it is expandable. In the resting position, the glans is retracted deeply into the truncus penis and during copulation (or artificially caused by hot lactic acid) internal pressure pushes the stylus forward and the membranous tubes are folded downwards (Figs. 41–42). This way the stylus can reach deeper into the female vagina during copulation.

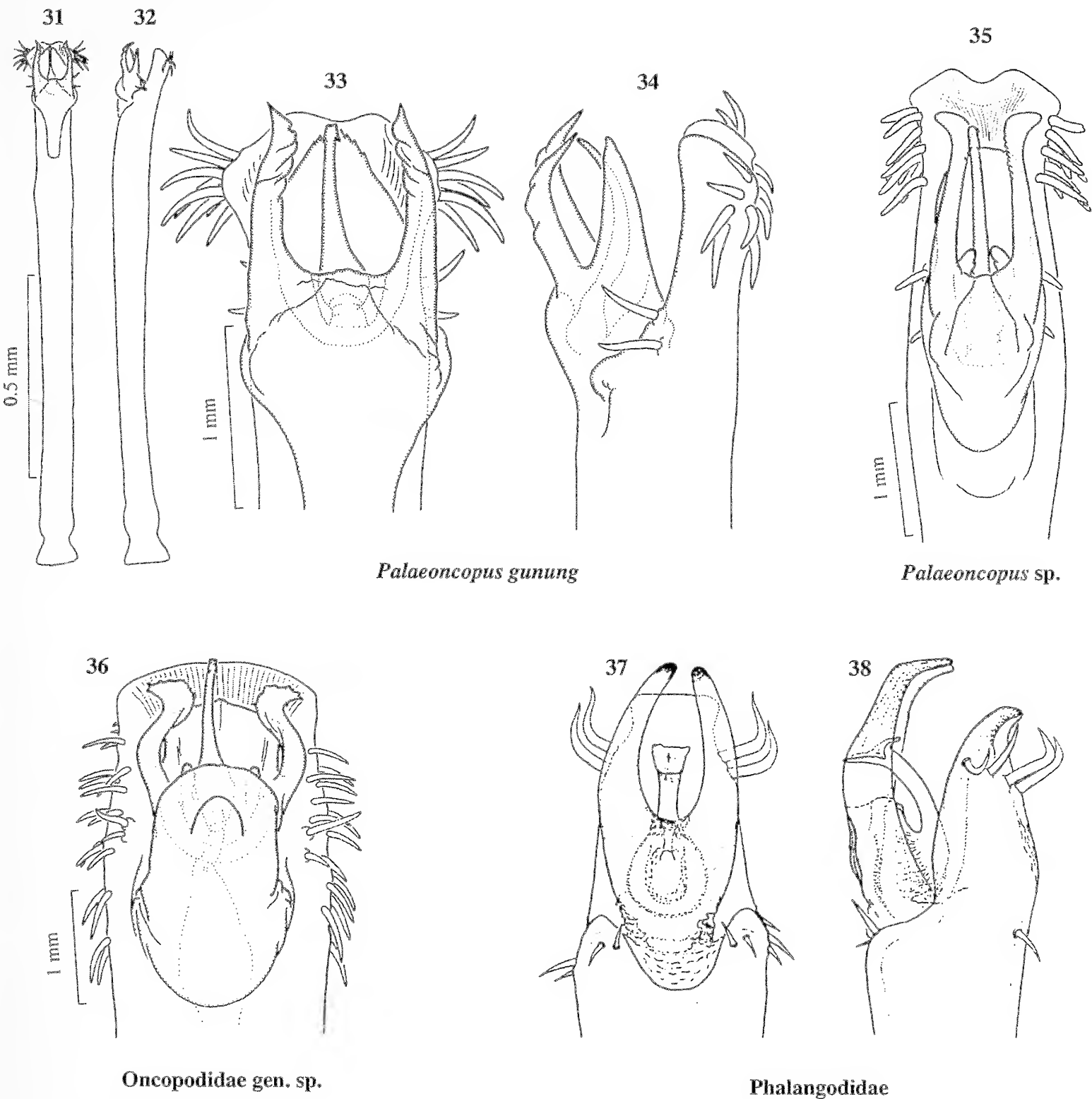
Penes with a distad-directed expandible glans are found in a number of laniatorean

families (e.g., Assamiidae, Podoctidae, Zalmoxidae, Biantidae), those of the Biantidae (Figs. 52–54; see also Martens 1986) are most comparable with *Biantoncopus*.

The penis of an undescribed oncopodid from Sarawak (Figs. 50–51) possesses a similar, expandible penis as *Biantoncopus fuscus*, but distinct differences in body shape and tarsal formula (1-1-2-2 instead of 2-2-3-3) place these two species generically apart.

An undescribed *Biantoncopus* sp. from the Philippines (Figs. 45–46) has its glans originating from far down the truncus penis and thus bears an additional resemblance with the penes of the Fissiphalliidae (Figs. 47–49; see also Martens 1988).

Type 3.—The species of *Gnomulus* and *Oncopus* show a penis form which was previously considered typical for the Oncopodidae. Here the glans is proximad-directed in its resting position (Figs. 1–22, 55, 56) and has to be folded upwards 180° for sperm transfer. This clearly presents an apomorphic situation. Considerable variation in the shape of penis and glans, with reduction of the median plate (Figs. 10, 13, 22) and enlargement of the stylus (Figs. 10, 13, 16, 22), exists within the



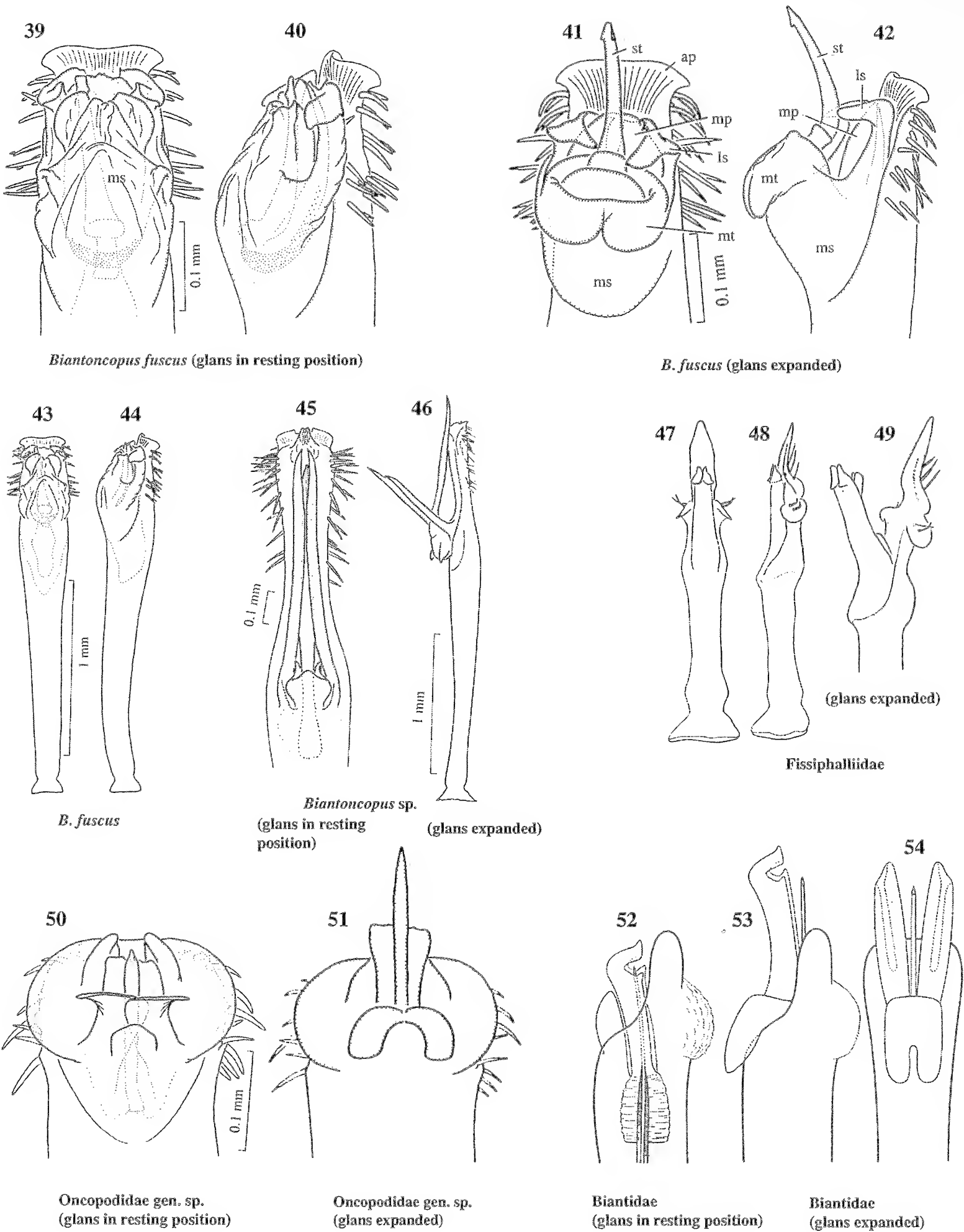
Figures 31–38.—31–36. Penis type 1: 31–34. *Palaeoncopus gunung*; 35. *Palaeoncopus* sp., an undescribed cave-dwelling species from northern Sumatra; 36. An undescribed oncopodid of uncertain relationships from Nepal; 37–38. *Haasus judaeus*, a phalangodid from Israel (from Martens 1976). 31. Total penis, dorsal view; 32. Total penis, lateral view (glans expanded); 33, 35–37. Apex of penis, dorsal view; 34 (glans expanded), 38. Apex of penis, lateral view.

species-rich genus *Gnomulus* (Figs. 5–22). The species of *Oncopus*, on the other hand, appear to be much more uniform in their penis structure (Figs. 1–4).

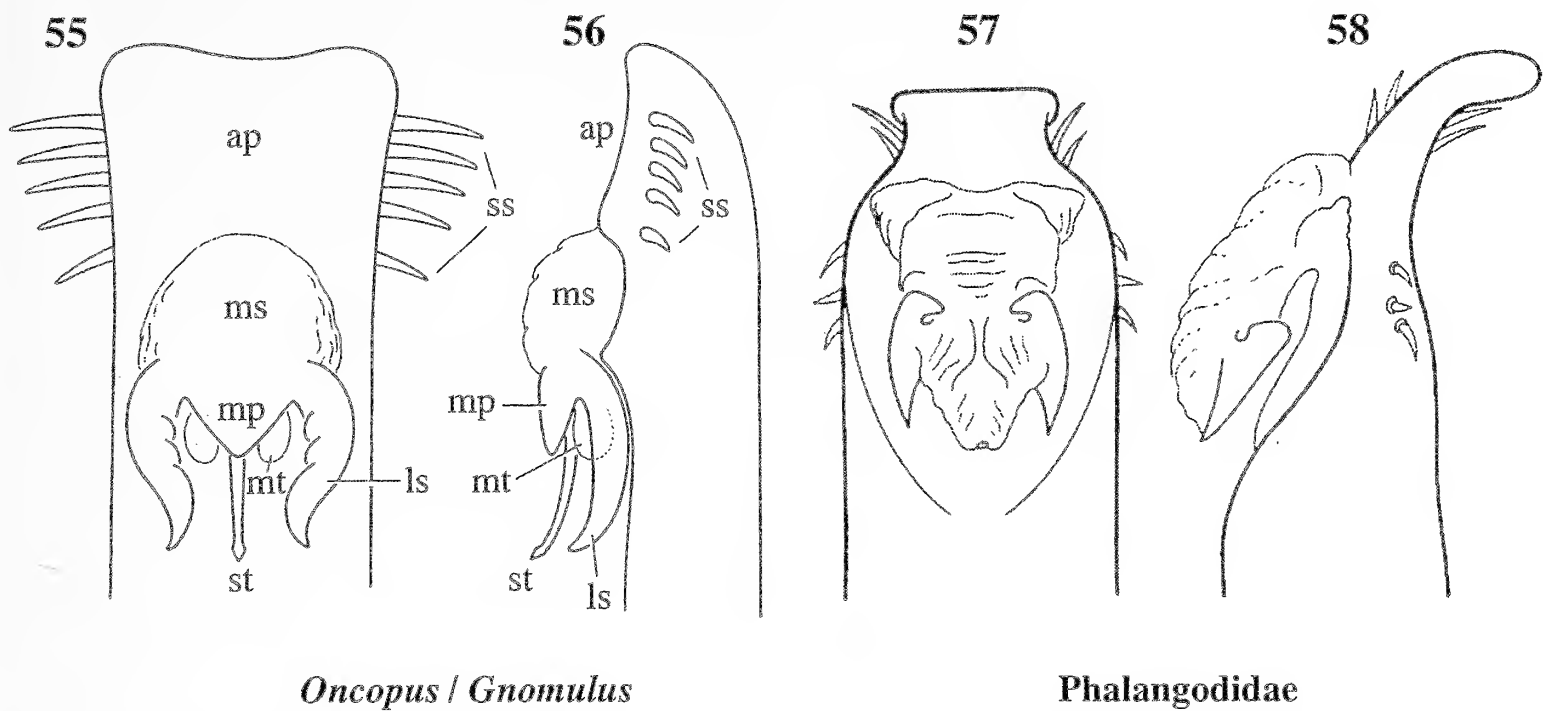
A comparable penis form with proximad-directed glans is found only in some species of the phalangodid genus *Scotolemon* Lucas 1860 in Europe (Figs. 57–58; see also Martens 1986).

Type 4.—*Caenoncopus* shows an extreme modification of the former penis type. Here

the stylus of the proximad-directed glans penis is asymmetrical and hypertrophied (Figs. 23–28), in one species almost reaching down to the base of the truncus (Figs. 23–24); the other elements of the glans are reduced (or fused with the stylus?). This penis type is highly apomorphic and truly unique among the Opiliones. Penes with a hypertrophied glans are elsewhere found in Triaenonychidae from Australia and South America (Figs. 29–30; see Hunt & Maury 1993), but there the



Figures 39–54.—39–44. *Biantoncopus fuscus*; 45–46. An undescribed *Biantoncopus* sp. from the Philippines; 50–51. An undescribed oncopodid from Sarawak; 47–49. *Fissiphallius sympatricus* Martens (Fissiphalliidae) (from Martens 1988); 52–54. Biantidae (from Martens 1986; generalized pattern). 43, 47. Total penis, dorsal view; 44, 46 (glans expanded), 48. Total penis, lateral view; 39, 41, 45, 50, 51, 54. Apex of penis, dorsal view (41, 51, 54 with glans expanded); 40, 42, 49, 53. Apex of penis, lateral view (42, 49, 53 with glans expanded). Abbreviations: ap = apex of truncus; ls = lateral sclerites; mp = median plate; ms = membranous socket; mt = membranous tubes; ss = subapical setae; st = stylus.



Figures 55–58.—55–56. Penis type 3: generalized scheme of an oncopodid penis of the *Gnomulus/Oncopus* type in resting position; 57, 58. *Scotolemon lespesi* Lucas (Phalangodidae) (from Martens 1986). 55, 57. Apex of penis, dorsal view; 56, 58. Apex of penis, lateral view. Abbreviations: ap = apex of truncus; ls = lateral sclerites; mp = median plate; ms = membranous socket; mt = membranous tubes; ss = subapical setae; st = stylus.

glans is terminal, distad-directed and symmetrical, and the truncus possesses a muscle (muscle-tendon type of penis). No close relationship exists between these two opilionid groups.

The Oncopodidae thus show the greatest variability in penis forms among opilionids known at present. In other laniatorean families we usually find only one penis type, with the exception of the polyphyletic Phalangodidae (Figs. 37, 38, 57, 58), the different penis forms of which, after a thorough revision, will probably be assigned to different families. In other opilionid families (e.g., Phalangiidae and Nemastomatidae), penis structures are quite diverse as well, but due to the muscle-

tendon principle of their penes, the glans is strictly positioned at the end of the truncus. There the variability in forms is expressed in, e.g., wing-like structures at the end of the truncus, highly diverse spinations of the glans, and/or a system of sclerites and membranes of a bulbous glans (Martens 1978). These modifications often look less spectacular than freely movable and inflatable glans structures in many “hemolymph-pressure Laniatores”, but they nevertheless represent the outcome of rich radiation processes as well.

Hypothetical evolution of penis types in the Oncopodidae.—How could this richness of penis forms in Oncopodidae have developed? A preliminary interpretation of genital

Table 1.—The characters (and their polarization) currently considered to be most informative for identifying phylogenetic relationships in Oncopodidae.

Characters	Plesiomorphic state	Apomorphic state
Glans orientation	distad-directed	proximad-directed
Glans function	non-expandible	expandible
Stylus size	thin	widened, hypertrophied
Stylus form	symmetrical	asymmetrical
Median plate	present	absent
Membranous tubes	present	absent
Truncus penis	narrow	apex widened
Anterior tarsi	1 article	2 articles
Posterior tarsi	3 articles	1 or 2 articles

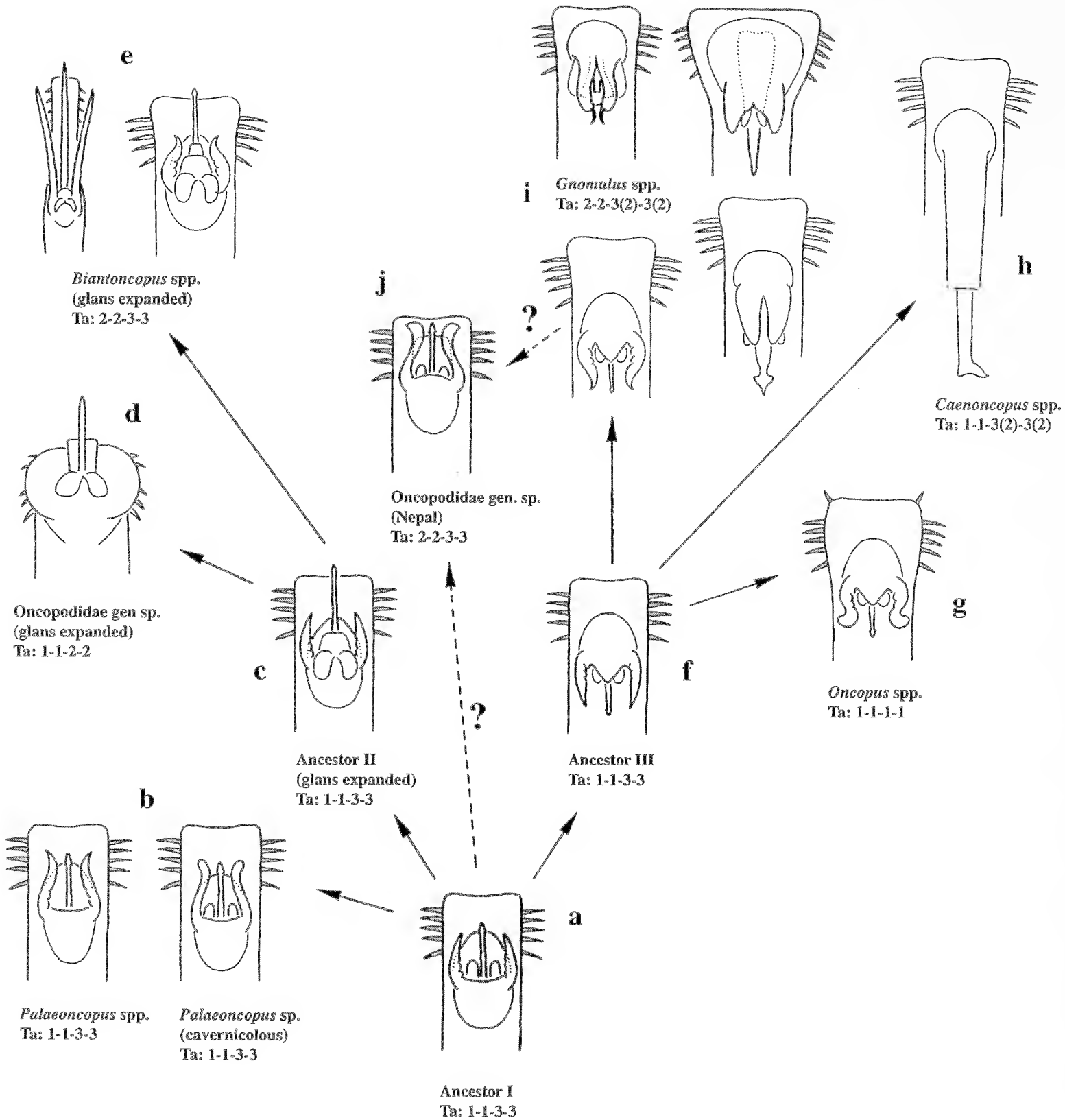


Figure 59.—Hypothetical evolution of the four penis types and presumed relationships in the Oncopodidae. Explanation given in the text (under "Hypothetical evolution of penis types in the Oncopodidae").

and external characters leads us to the following hypothetical evolution illustrated in Fig. 59 (modified after Martens & Schwendinger 1998: fig. 134). Shape of glans penis and tarsal formula are given as the most informative traits; character polarization is shown in Table 1.

From an ancestral taxon with a short, distad-directed, non-expandable glans and tarsal formula 1-1-3-3 (Fig. 59a), three phylogenetic lineages diverged. One development led to the basic *Palaeoncopus*, which remained quite

primitive apart from a reduction of the membranous tubes of the glans in 3 out of 4 species examined (Fig. 59b). A second lineage first acquired an expandable (still distad-directed) glans in a second, later ancestor (Fig. 59c) then split into terminal genera, one with a reduced number of tarsalia on posterior legs (Fig. 59d) and the other, *Biantoncopus*, with an increased number of tarsalia on anterior legs (Fig. 59e). The third lineage first had its glans transposed to a proximad-directed po-

sition in a third ancestral taxon (Fig. 59f) and then split into 3 extant genera: *Oncopus* with an unmodified glans and posterior tarsalia reduced to one article (Fig. 59g), *Caenoncopus* with a strongly modified glans (asymmetrical, hypertrophied stylus) and a primitive tarsal formula (posterior tarsalia apomorphically reduced to 2 in one species) (Fig. 59h) and *Gnomulus* with a primitive glans (but several modifications and reductions in individual species) and anterior tarsi increased to two (posterior tarsalia additionally reduced to 2 in a few species) (Fig. 59i).

The relationships of an undescribed species from Nepal are uncertain. Its distad-directed glans indicates a basic position within the Oncopodidae, whereas derived external characters (e.g., tarsal formula 2-2-3-3) point towards a more derived position (Fig. 59j). Due to striking resemblance in external morphology with species of the *Gnomulus aborensis*-group, we provisionally consider this undescribed taxon as an aberrant *Gnomulus*, which has undergone a reversal in its glans direction.

DISCUSSION

This interpretation of penis evolution also reflects our present view of relationships within the Oncopodidae. However, the picture that we draw is only preliminary and not the result of a thorough cladistic analysis. Some of the available but yet undescribed taxa have not yet been studied in great detail and further new oncopodids will probably be discovered in the near future, which may change the current picture considerably. A more detailed and thorough analysis of oncopodid relationships will thus be given at the end of our ongoing revision of this family.

At this stage, however, we feel safe to say that the Oncopodidae is, with respect to penis morphology, clearly the most diverse opilionid family. Penis forms range from quite primitive (in comparison with other Laniatores) to the most highly derived in opilionids, a range which in other Laniatores stretches over at least three different families.

Relationships with other families still remain unclear, but in view of primitive external morphology and a very wide range in penis morphology, the Oncopodidae can still be regarded as the sister group of the Gonyleptoidea, i.e. the remaining Laniatores with "hemolymph-pressure" penes. Consequently it

appears justified to claim superfamily rank for the Oncopodidae, as proposed by Martens (1976). This we have questioned in one of our preceding papers (Martens & Schwendinger 1998:502).

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Mrs Käthe Rehbinder (Mainz) produced Figs. 55 and 56 of this paper and Lionel Monod (Geneva) helped with the graphical presentation of illustrations. The City of Geneva (through the Natural History Museum of Geneva) kindly supported P.J.S.'s participation in the 15th International Congress of Arachnology in Badplaas, South Africa. The German Academic Exchange Service (Deutscher Akademischer Austauschdienst, Bonn) supported P.J.S. with a one month grant to carry out research work in Mainz. The Feldbausch Foundation of the University of Mainz provided travel funds to J.M.

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THE HARVESTMAN FAMILY PHALANGODIDAE 4. A REVIEW OF THE GENUS *BANKSULA* (OPILIONES, LANIATORES)

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ABSTRACT. Two new species of *Banksula* are described. *Banksula incredula* enlarges the concept of the genus and is assigned to a new species group which is the likely sister group to the other *Banksula*. The species is unique in numerous morphological features, being the largest species in the genus, the first non-cavernicolous species, and occurring in the Coast Ranges of California, rather than in the Sierra Nevada foothills. The second new species, *B. tutankhamen*, is a typical member of the *californica* group but with more pronounced troglomorphy. Clinal variation is documented for *B. grahami* Briggs 1974, with *B. elliotti* Briggs & Ubick 1981, now placed as its junior synonym, representing the northern and most troglomorphic populations.

Keywords: *Banksula*, Phalangodidae, Opiliones, cavernicoles, California

The phalangodid genus *Banksula* Roewer 1949 was established for *Scotolemon californica* Banks 1900, a troglobitic species from Alabaster Cave in the Sierra Nevada, California. Eight additional species were subsequently added by Briggs (1974) and Briggs & Ubick (1981). Although some of these have large apparently functional eyes, all are restricted to the caves of the central Sierra Nevada foothills. Given the narrow distribution and habitat preference for the genus, it came as quite a surprise to discover an epigeal species, and especially one from the Coast Ranges of California. This species, which we are describing here as *Banksula incredula* new species, also extends the generic limits on morphological grounds, being the largest species in the genus and having a leg hypertrophy which, in some individuals at least, exceeds that of most troglobitic *Banksula*. Despite these and other unique features, which are discussed below, the species is clearly a member of the genus *Banksula* given that its palpal femur bears a dorsal row of setose tubercles (Figs. 2, 3). Although similar tubercles occur in some species of *Sitalcina* (Figs. 4, 5), these do not bear setae and thus are not homologous to those in *Banksula*. Also, and even more fundamentally, the penis of *B. incredula* is typical of *Banksula*, having a bifurcate ventral plate with ventrally situated prongs and a rel-

atively simple glans consisting of a stylus and a pair of parastylar lobes (Figs. 18–22).

METHODS

Specimen preparation and observation follows the format described in earlier papers (Briggs & Ubick 1981; Ubick & Briggs 1989). All measurements not labeled otherwise are in millimeters. ‘Fig.’ and ‘Figs.’ refer to this paper, ‘fig’ and ‘figs’ to previously published works.

All specimens are deposited at the California Academy of Sciences, San Francisco, California, apart from the type series of *Banksula californica* (Banks), which is at the Museum of Comparative Zoology, Cambridge, Massachusetts.

The following abbreviations are utilized: AS = apical spine of VPP; AT = apical tooth of ovipositor; EMH = eyemound height; EML = eyemound length; GO = genital operculum; GOW = genital operculum width; PSL = parastylar lobes; SL = scute length; SW = scute width; TBL = total body length; TC = tarsal count; VP = ventral plate; VPP = ventral plate prong; VPW = VPP width.

TAXONOMY

Genus *Banksula* Roewer

Banksula Roewer 1949: 33; Briggs 1974: 1; Briggs & Ubick 1981: 315.

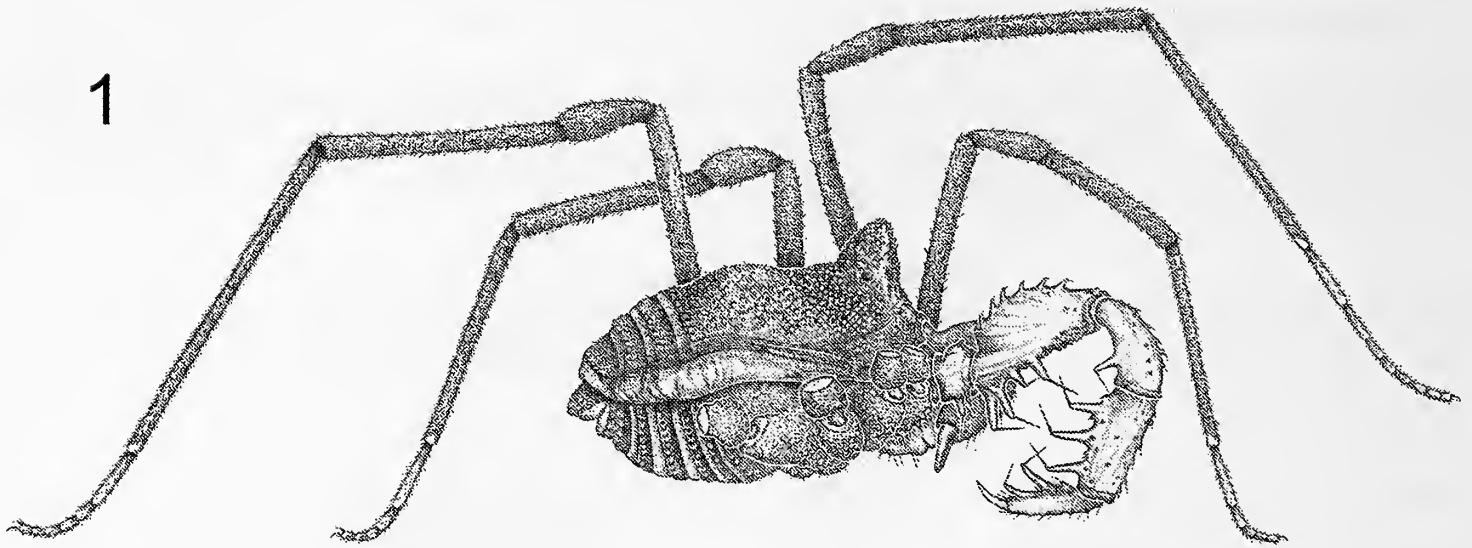


Figure 1.—*Banksula incredula*, lateral view (drawing by Jenny Speckels).

Type species.—*Scotolemon californica* Banks 1900.

Diagnosis.—Species of *Banksula* are unique among the Nearctic Phalangodidae in having a row of setiferous dorsal tubercles on the palpal femur (Figs 2, 3) and a penis with a bifurcate ventral plate with ventrally positioned prongs (Figs. 18, 19).

Description.—Color of body yellowish to orange; appendages white to yellowish white. Body length 1.5–3.0 mm. Body covered with tubercles. Scute with eyemound low and rounded to high and conical; cornea and retina present or absent. Anterior margin of scute with 0 to a few pairs of small anterior tubercles; ozopores lateral. Palpal megaspines: femur with one to two mesodistal and three to four ectobasal; patella with two mesal and one ectal; tibia with three mesal and three ectal; tarsus with two mesal and two ectal. Palp with dorsal row of setiferous tubercles on femur and smaller tubercles dorsally on other segments, laterally on femur, and between megaspines; basal megaspine of femur with mesal and ectal tubercles in most species, mesal tubercle absent in most females. Tarsal count 4–6–5–6, in most species, and 4 or 5–7 to 9–5–5 or 6 in *B. incredula*. Ovipositor surface wrinkled; smooth or covered with microspines; apical teeth present or absent; with 6 pairs of apical and 1 pair of subapical setae; setae slightly curved, apically pointed. Penis with folding glans; stylus short, narrow or wide, with lateral carinae present or absent, surrounded by 1 pair of parastylar lobes; ventral plate bifurcate, with 1 pair of apical spines, 7–12 pairs of long setae and up to 12 pairs of short setae.

The *incredula* species group

Diagnosis.—The single species representing this group differs from other *Banksula* in several characters: it is large, has a higher tarsal count, occupies an epigeic habitat, has large eyes and a high eyemound, and has additional palpal megaspines, with 4 ectobasal and 2 mesoapical on the femur. As regards the genitalia, males have a ventral plate with large apical spines and long setae and females an ovipositor with smooth cuticle and a pair of apical teeth.

Distribution.—Known only from a single locality in San Mateo County, California.

Banksula incredula new species

Figs. 1–3, 6, 9–22

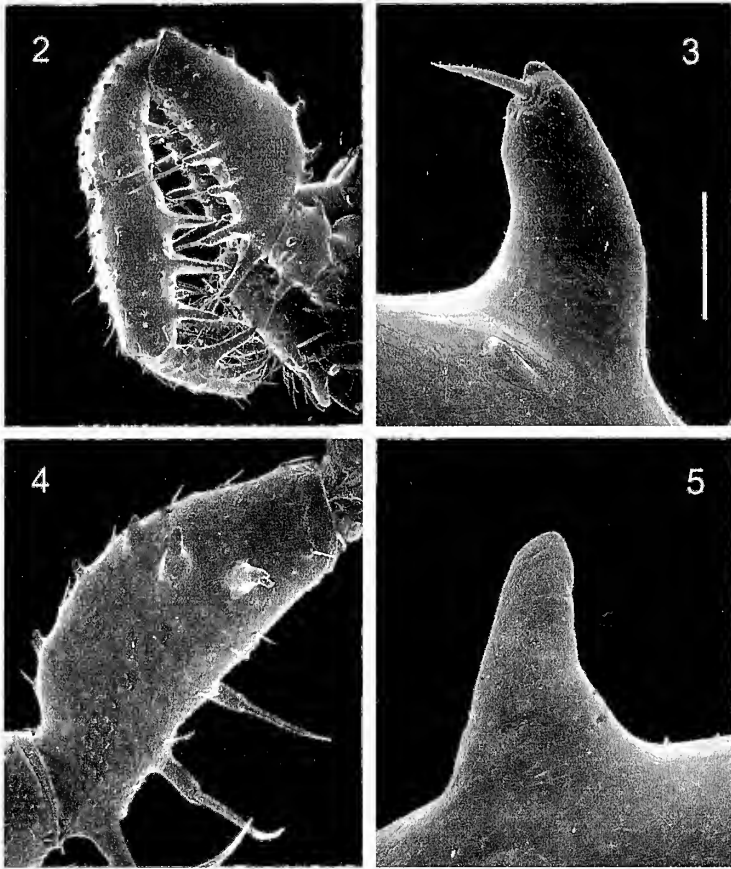
Type.—Male holotype from within a sandstone talus on San Bruno Mountain, San Mateo County, California (10 May 1991; D Ubick) deposited in CAS.

Etymology.—The species name refers to the unexpected morphology, habitat, and distribution of the species, and is considered feminine in gender.

Diagnosis.—Same as for species group.

Description.—Total body length, 2.56–3.00. Scute length, 1.79–2.18. Leg II length, 8.81–10.51. Leg II/Scute length, 4.64–5.64. Tarsal count, 4 to 5–7 to 9–5–5 to 6. (N = 8)

Color orange, appendages pale orange, tarsi white. Body uniformly coarsely tuberculate. Scute margin without apparent anterior tubercles. Eyemound a prominent cone, as high as long. Cornea and retina large and conspicuous. Genital operculum relatively small: $GOW/SW = 0.2$. Palpal megaspines: femur



Figures 2–5.—Phalangodid palpi. 2, *Banksula incredula*, lateral view of male left palp; 3, same, close-up showing dorsal femoral tubercle; 4, *Sitalcina chalona* Briggs, lateral view of male left palpal femur; 5, same, close-up showing dorsal tubercle. Scale bar: 2 = 610 μm ; 3 = 38 μm ; 4 = 150 μm ; 5 = 30 μm .

with 4 ventrobasal and 2 mesodistal; patella with 1 ectal and 2 mesal; tibia with 3 ectal and 3 mesal; tarsus with 2 ectal and 2 mesal. Palpal femur with 5–7 setiferous tubercles dorsally.

Male (holotype): Total body length, 2.59. Scute length, 2.18; width, 2.01. Eyemound length, 0.49; width, 0.64; height, 0.49. Oper-

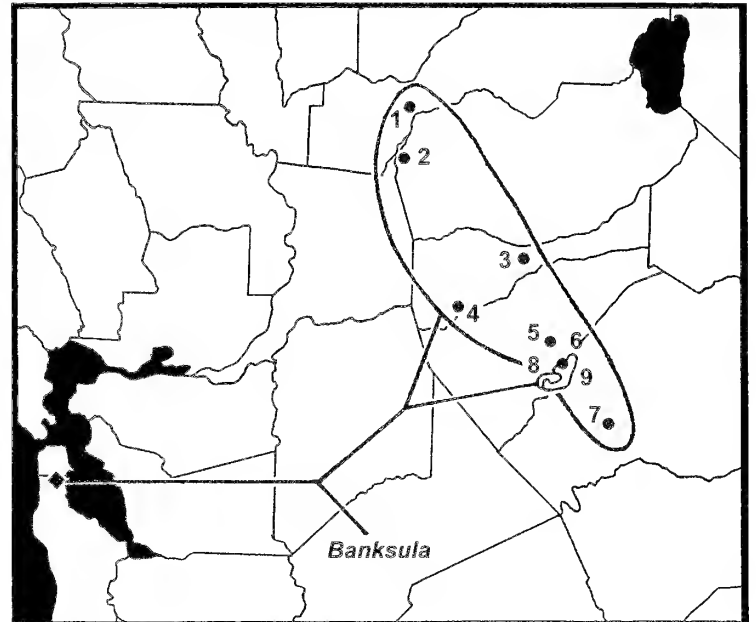
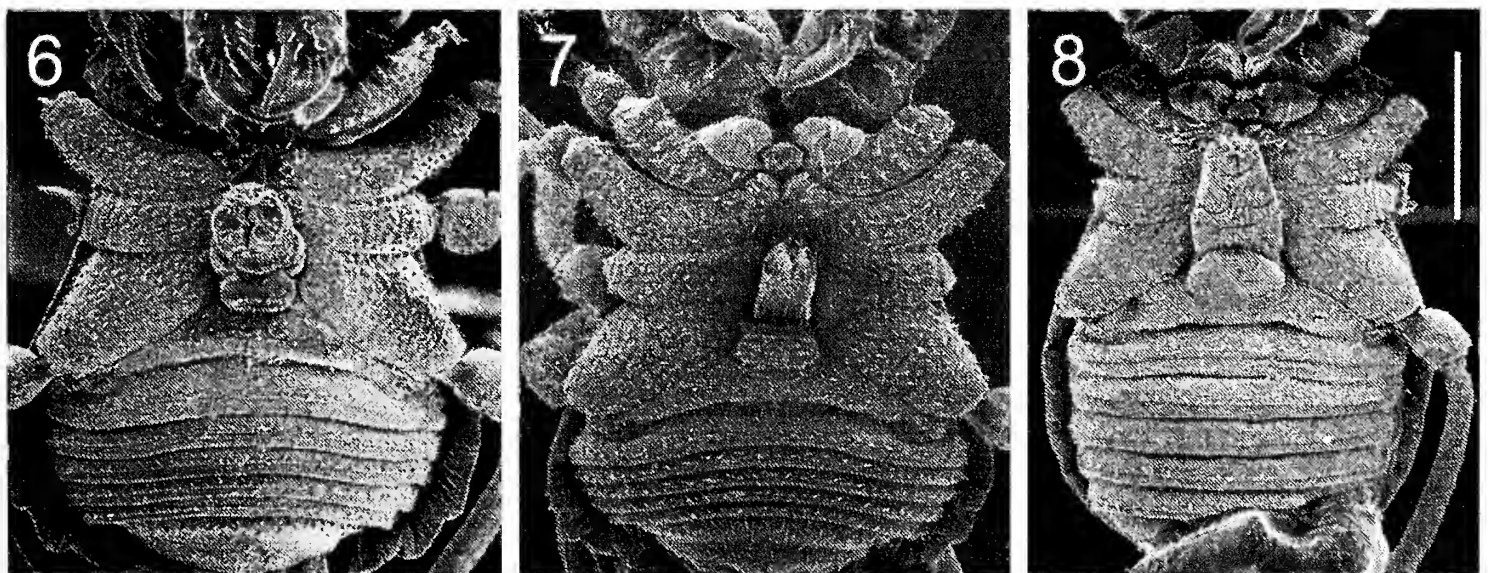


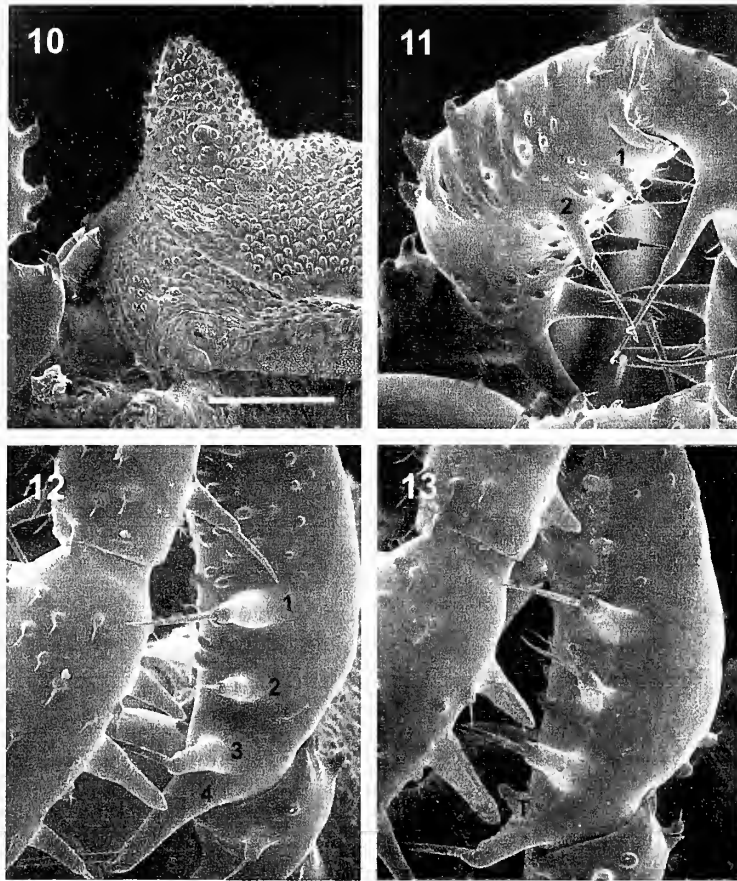
Figure 9.—Map of central California showing distribution and area cladogram of *Banksula*. Symbols: diamond = *B. incredula*; dots = *B. californica* group (1, *B. galilei*; 2, *B. californica*; 3, *B. grubbsi*; 4, *B. rudolphi*; 5, *B. tutankhamen*; 6, *B. martinorum*; 7, *B. tuolumne*); oblong region = *B. melones* group (8, *B. melones*; 9, *B. grahami*).

culum width, 0.32. Leg II length, 10.12. Leg II/scute length, 4.64. Tarsal count, 5–8 and 9—5–6. Proximal megaspine of palpal femur with mesal tubercle at base; lacking ectal tubercle.

Penis (Figs. 18–22): VPP subparallel, separated by width of one prong; with large slightly curved AS; with 10 long setae in apical half and 12 short setae basally on each prong; long setae clearly longer than to twice the length of AS; short setae about half the length of AS. Glans with apical stylar region consisting of triangular pointed stylus and a pair of ribbon-like apically rounded PSL.



Figures 6–8.—Venters of female *Banksula* representing the three species groups. 6, *B. incredula*; 7, *B. galilei* (*californica* group); 8, *B. melones*. Scale bar: 6 = 750 μm ; 7 = 430 μm ; 8 = 600 μm .



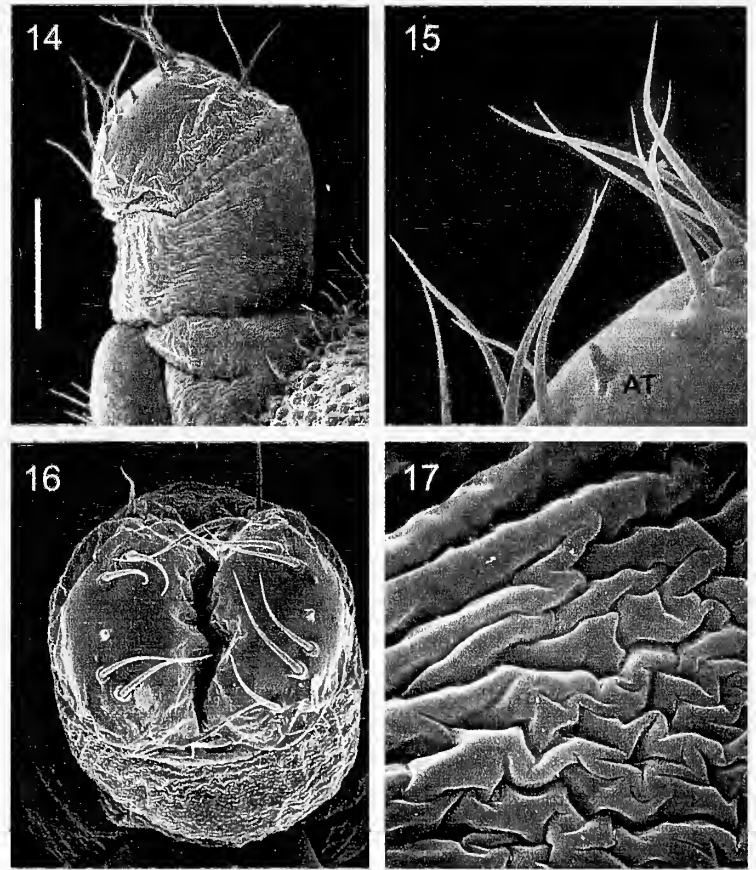
Figures 10–13.—*Banksula incredula*. 10, anterior half of female scute showing eyemound; 11, female left palp showing two mesoapical megaspines (1, 2); 12, female left palp showing four ectobasal megaspines (1, 2, 3, 4); 13, male left palp showing mesal tubercle (M) on ventral megaspine. Scale bar: 10 = 430 μ m; 11–13 = 300 μ m.

Female (paratype): Total body length, 2.92. Scute length, 1.87; width, 1.95. Eyemound length, 0.36; width, 0.51; height, 0.41. Leg II length, 8.81. Leg II/scute length, 4.71. Tarsal count, 4–7 and 8–5–5 and 6.

Ovipositor (Figs. 6, 14–17): cuticle smooth, wrinkled laterally; apex with 12 apical setae arranged in 4 triads, 1 pair of subapical dorsal setae, and 1 pair of apical teeth.

Sexual dimorphism.—The patellar ectal megaspine is slightly shorter in males, being about 1/2 the length (as opposed to about 2/3, in females) of the tibial ectobasal megaspine. Females lack both mesal and ectal tubercles at the proximal megaspine of the palpal femur.

Juveniles.—Two juvenile specimens were collected with the adults, and several others were observed. The later instar is white with slight yellowish pigmentation on the posterior half of the abdomen; integument smooth; chelicerae lacking ectobasal knob; retina and cornea present; palpal megaspines as in adult; and tarsi III and IV with two claws and large areoleum. Measurements: TBL, 1.72; SL, 1.38;



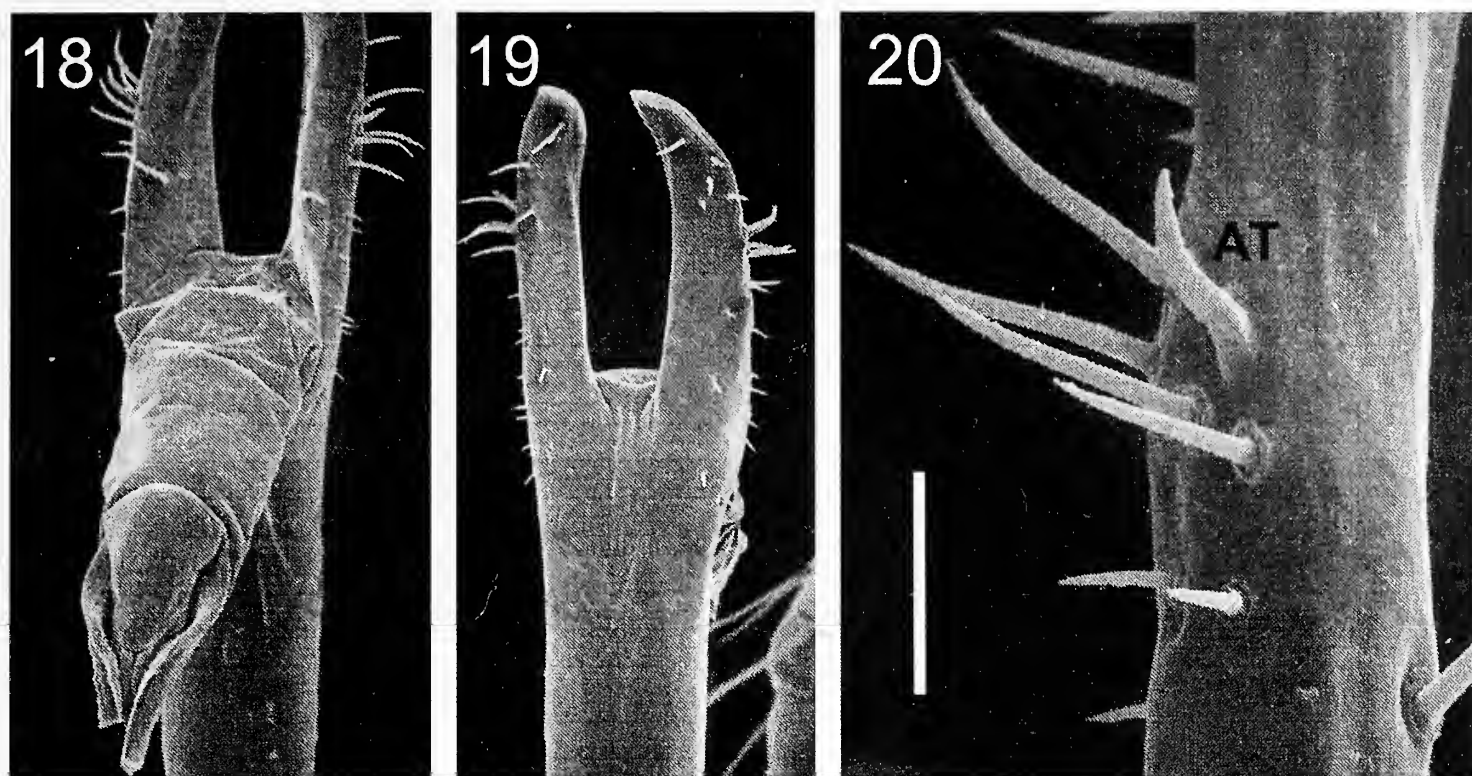
Figures 14–17.—*Banksula incredula*, ovipositor. 14, lateral view; 15, close-up showing apical tooth (AT); 16, apical view; 17, close-up of lateral surface showing absence of misrospines. Scale bar: 14 = 200 μ m; 15 = 60 μ m; 16 = 150 μ m; 17 = 20 μ m.

SW, 1.28; EML 0.23; EMH 0.21; GOW / SW, 0.16; Leg II, 7.31; Leg II/SL, 5.30; TC, 2–2–3–3.

The other instar is similar in appearance but smaller. Measurements: TBL, 1.31; SL, 1.10; SW, 1.28; Leg II, 7.97; Leg II/SL, 7.25; TC, 2–2–3–3.

Remarks.—This species is known only from a single trailside talus slope of Franciscan sandstone with a dense chaparral canopy on the north slope of San Bruno Mountain ridge. The talus is not a natural exposure but was artificially excavated during the installation of a gas pipeline several decades ago. Collecting at similar talus areas along other sections of this pipeline at San Bruno Mountain, as well as other localities along the central Coast Ranges, has not yielded additional *Banksula*. Specimens were found in the talus cavities along with other phalangodid harvestmen (*Sitalcina californica* (Banks) and *Microcina* sp.) and troglomorphic spiders (*Nesticus silvestrii* Fage, *Archoleptoneta schusteri* Gertsch, and *Blabomma* sp.).

Material examined.—All from the type locality: 1 ♀ (10 May 1991, D. Ubick); 3 ♂, 3 ♀, 2 juveniles (11 May 1991, T. Briggs, D.



Figures 18–20.—*Banksula incredula*, penis. 18, dorsal view; 19, ventral view; 20, dorsal view of left ventral plate prong showing apical spine (AS). Scale bar: 18, 19 = 150 μ m; 20 = 30 μ m.

Ubick); 1 ♀ (18 Jan. 1992, T. Briggs, W. Rauscher, D. Ubick); 1 ♂, 1 ♀ (26 Jan. 1992, T. Briggs, W. Savary, D. Ubick).

The *californica* species group

Diagnosis.—Members of this group are distinguished from *B. incredula* in being smaller, having a relatively lower and uniform TC of 4–6–5–6, and a palpal femur with only 3 ventrobasal and 1 mesoapical mega-

spines. They differ from the *melones* group in having a smaller GO, with a GO/SW ratio of 0.2 as opposed to 0.3, and in having sexually dimorphic palpi, with males having enlarged femora and reduced ectal megaspines on the tibia and patella (Fig. 44, 45).

Included species.—*Banksula californica* (Banks 1900), *Banksula galilei* Briggs 1974, *Banksula grubbsi* Briggs & Ubick 1981, *Banksula martinorum* Briggs & Ubick 1981, *Banksula rudolphi* Briggs & Ubick 1981, *Banksula tuolumne* Briggs 1974 and *Banksula tutankhamen* new species.

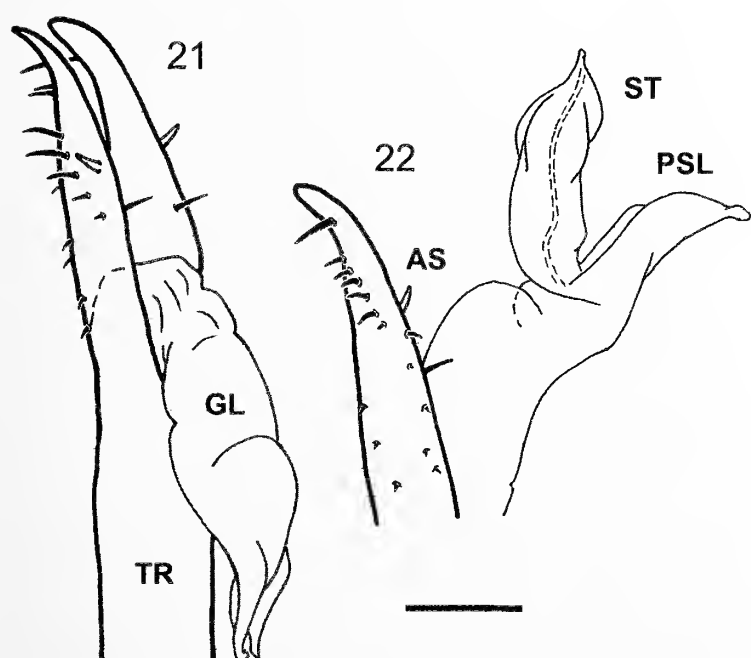
Variation.—The species of the *californica* group are morphologically very similar, including in details of the genitalia, and were we to use the same criteria of distinctness as for other phalangodids (i.e., *Calicina* and most *Texella*) the number of species here could be reduced to just one. However, given that the species are strongly disjunct, being found in isolated caves, and because of the presence of distinct, if minor, differences in their somatic and genitalic features, we are here recognizing them all as valid.

Distribution.—Known from caves in the Sierran Motherlode Region from Placer to Tuolumne Counties, California.

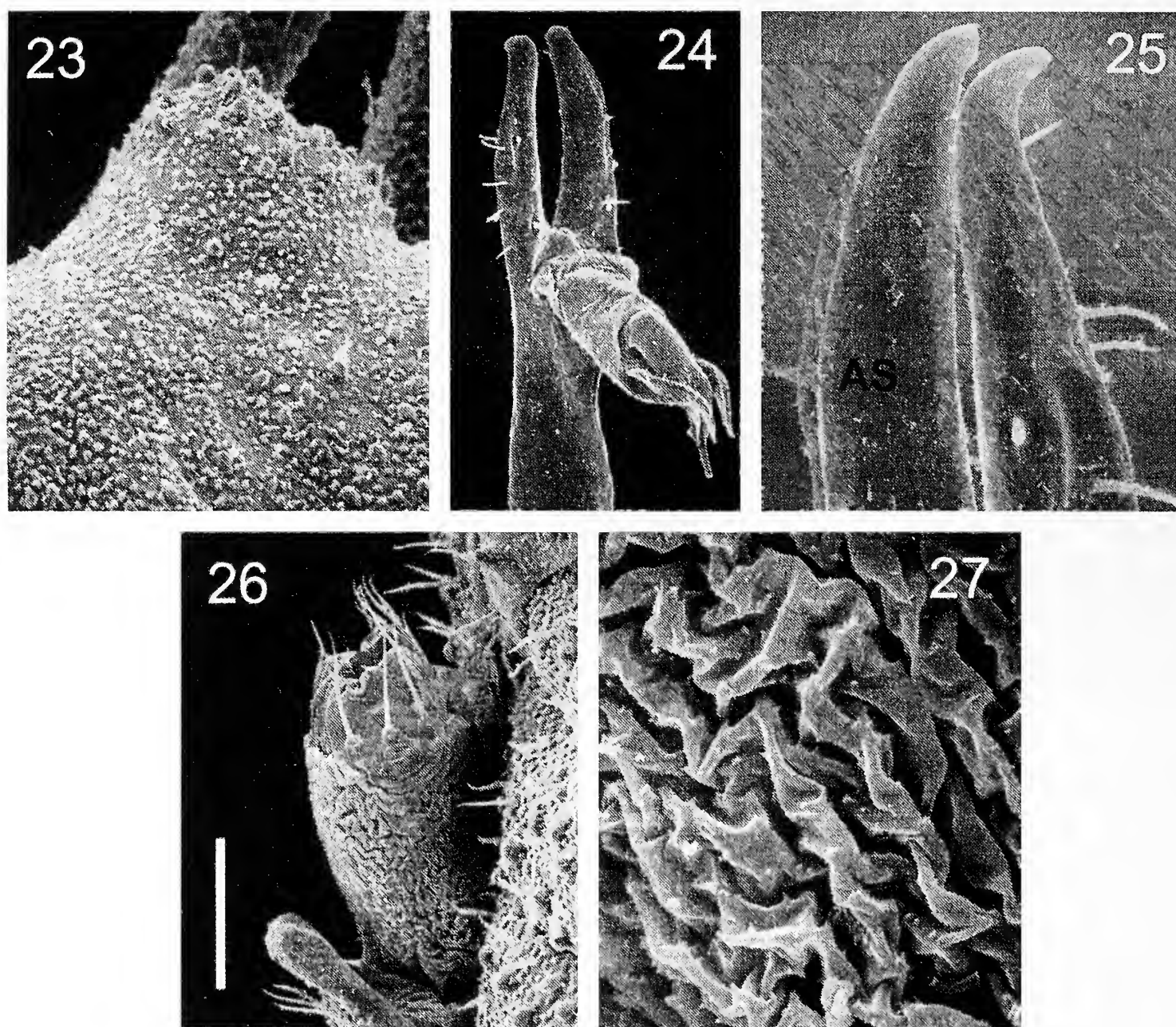
Banksula galilei Briggs

Figs. 7, 9, 23–27

Banksula galilei Briggs 1974: 6; Briggs & Ubick 1981: 316.



Figures 21–22.—*Banksula incredula*, lateral view of penis. 21, unexpanded glans (GL) and truncus (TR); 22, expanded glans showing stylus (ST), parastylar lobes (PSL), and apical spine (AS). Scale bar = 100 μ m.



Figures 23–27.—*Banksula galilei*. 23, eyemound of female showing absence of cornea (anterior to left); 24, dorsolateral view of penis; 25, close-up of ventral plate prong showing small apical spine (AS); 26, lateral view of ovipositor; 27, close-up of lateral surface of ovipositor showing microspines. Scale bar: 23, 24, 26 = 100 μ m; 25 = 25 μ m; 27 = 15 μ m.

Diagnosis.—This species differs from others in the *californica* species group by its obliquely truncate eyemound, dark retina, and a short AS.

Additional description.—Eyemound H/L 0.50, eye with dark retina and small cornea. Proximal megaspine of palpal femur with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with mesal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis: AS relatively short (AS/VPP width about 0.2); VPP with 7–9 long setae; VPP distal separation less than prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base.

Material examined.—All nine known specimens.

Distribution.—Known only from the Lime Rock Caves, near Auburn, Placer County, California.

Banksula californica (Banks)

Fig. 9

Scotolemon californica Banks 1900:200.

Banksula californica (Banks): Roewer 1949:33; Briggs 1974:4; Briggs & Ubick 1981:315.

Diagnosis.—This species differs from others in the *californica* species group in having a low rounded eyemound, eye lacking retina, and female palp with a somewhat reduced ectal tubercle at the base of the proximal megaspine.

Additional description.—Eyemound H/L 0.55, eyes without retina and with small, degenerate cornea. Palpal femur with 5–7 dorsal setiferous tubercles; proximal megaspine with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with curved ectal and robust mesal tubercle; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis with VPP distal separation about equal to prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base; ectal tubercle reduced, not curved at apex. Ovipositors not expanded in the fragile specimens available.

Material examined.—El Dorado County, Alabaster Cave (Marx, MCZ), ♀ lectotype, 3 ♂, 1 ♀ paralectotypes.

Distribution.—Known only from Alabaster Cave.

Remarks.—Alabaster Cave has been partially destroyed by mining and as the remaining portions have been sealed off with concrete, it is not possible to determine whether the species still survives.

Banksula grubbsi Briggs & Ubick

Fig. 9

Banksula grubbsi Briggs & Ubick 1981: 319.

Diagnosis.—This species differs from others in the *californica* species group by its obliquely truncate eyemound lacking retina and a low rounded ectal tubercle at the base of the proximal megaspine of the palpal femur.

Additional description.—Eyemound H/L 0.60, eye without retina and with degenerate cornea.

Male: Proximal megaspine of palpal femur with mesal tubercle and low, rounded ectal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines reduced. Penis with VPP distal separation about equal to prong width.

Female: Unknown.

Material examined.—The male holotype.

Distribution.—Known only from Black Chasm Cave, near Volcano, Amador County, California.

Banksula rudolphi Briggs & Ubick

Figs. 9, 28–32

Banksula rudolphi Briggs & Ubick 1981: 316.

Diagnosis.—This species differs from others

in the *californica* species group by its relatively tuberculate subconical eyemound, absence of retina, and presence of an ectal tubercle at the proximal megaspine of the palpal femur in both sexes.

Additional description.—Eyemound H/L 0.62, eye lacking retina and with degenerate cornea. Proximal megaspine of palpal femur with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with mesal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis: AS relatively short (AS/VPP width about 0.4); VPP with 9 long setae; VPP distal separation about equal to or wider than prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base.

Material examined.—The 36 known specimens.

Distribution.—Known only from Chrome Cave, near Pardee Reservoir, Amador County, California.

Banksula tutankhamen new species

Figs. 9, 33–40

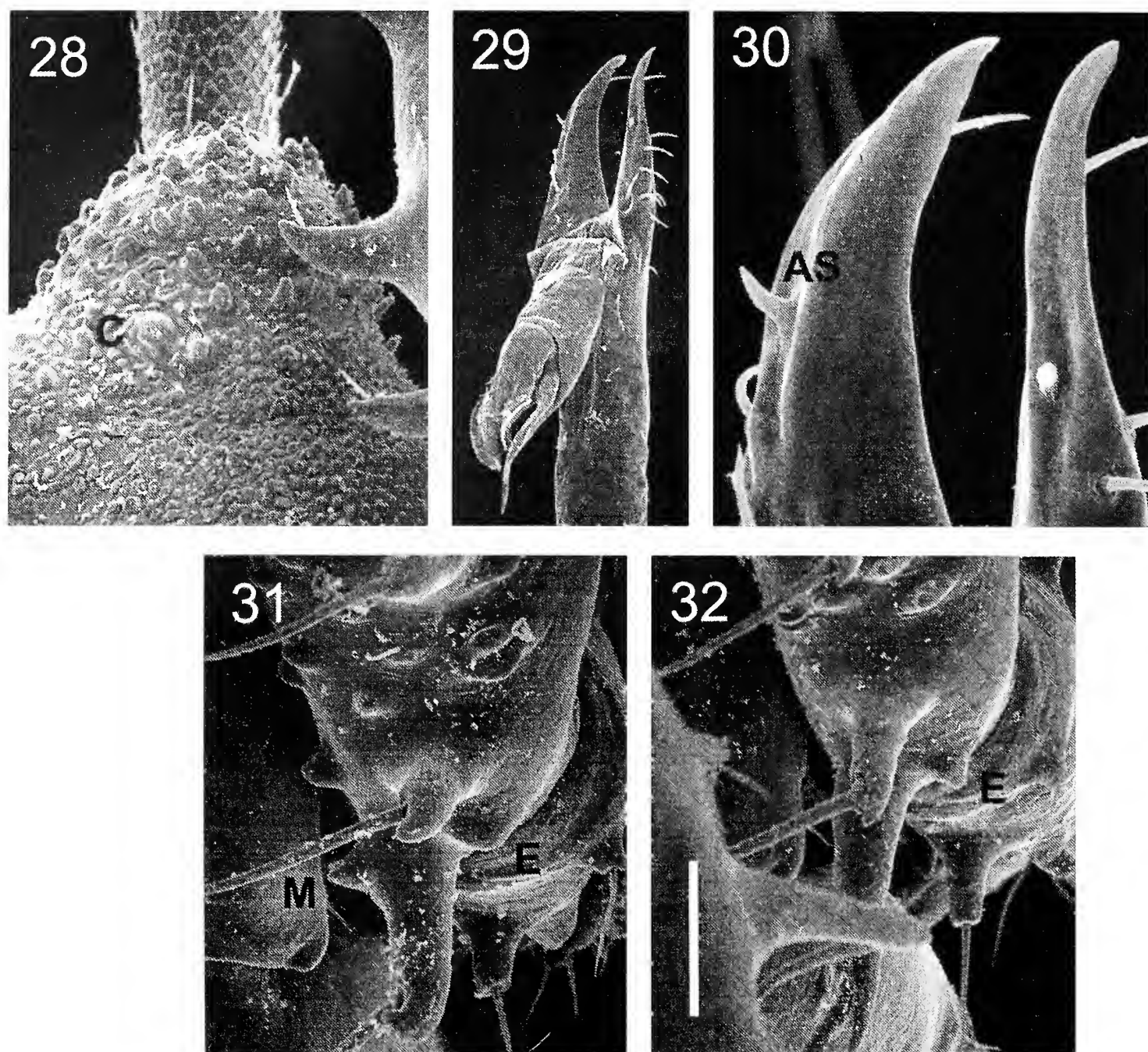
Type.—Male holotype from King Tut Cave, near Cave City and O'Neil Creek, Calaveras County, California (24 Aug. 1991; T. Briggs, D. Cowan, G. Malliet, W. Rauscher, D. Ubick), deposited in CAS.

Etymology.—The species name refers to the type locality.

Diagnosis.—This species differs from all other *Banksula* by its longer legs (having the highest Leg II/Scute length ratio in the genus) and in the tuberculation at the basal megaspine of the palpal femora, where the male has an enlarged or double mesal tubercle and both sexes lack an ectal one.

Description.—Total body length, 1.45–1.54. Scute length, 1.00–1.14. Leg II length, 6.45–6.77. Leg II/Scute length, 5.94–6.45. Tarsal count, 4–6–5–6. (N = 3)

Color yellow to pale yellow. Scute with segmentation delineated by small tubercles, lateral anterior margins with numerous tubercles; eyemound and area behind tuberculate. Eyemound subconical with retina and cornea degenerate. Genital operculum small; GOW/SW, 0.2. Palpal megaspines: femur with 3 ventrobasal and 1 mesodistal; patella with 1 ectal and 2 mesal; tibia with 3 ectal and 3



Figures 28–32.—*Banksula rudolphi*. 28, eyemound of male showing small cornea (C)(anterior to right); 29, dorsolateral view of penis; 30, close-up of ventral plate prong showing medium-sized apical spine (AS); 31, ventrobasal portion of male palpal femur showing mesal (M) and ectal (E) tubercles at basal megaspine; 32, ventrobasal portion of female palpal femur showing ectal (E) tubercle at basal megaspine. Scale bar: 28, 29, 31, 32 = 100 μm ; 30 = 25 μm .

mesal; tarsus with 2 ectal and 2 mesal. Palpal femur with 7 setiferous tubercles dorsally, apical pair transversely to subtransversely arranged. Proximal megaspine of palpal femur lacking ectal tubercle (except on one palp of a single male).

Male (holotype): Total body length, 1.45. Scute length, 1.09; width, 1.18. Eyemound length, 0.23; width, 0.41; height, 0.18. Leg II length, 6.68. Leg II/Scute length, 6.13. Proximal megaspine of palpal femur with enlarged or double tubercle mesally.

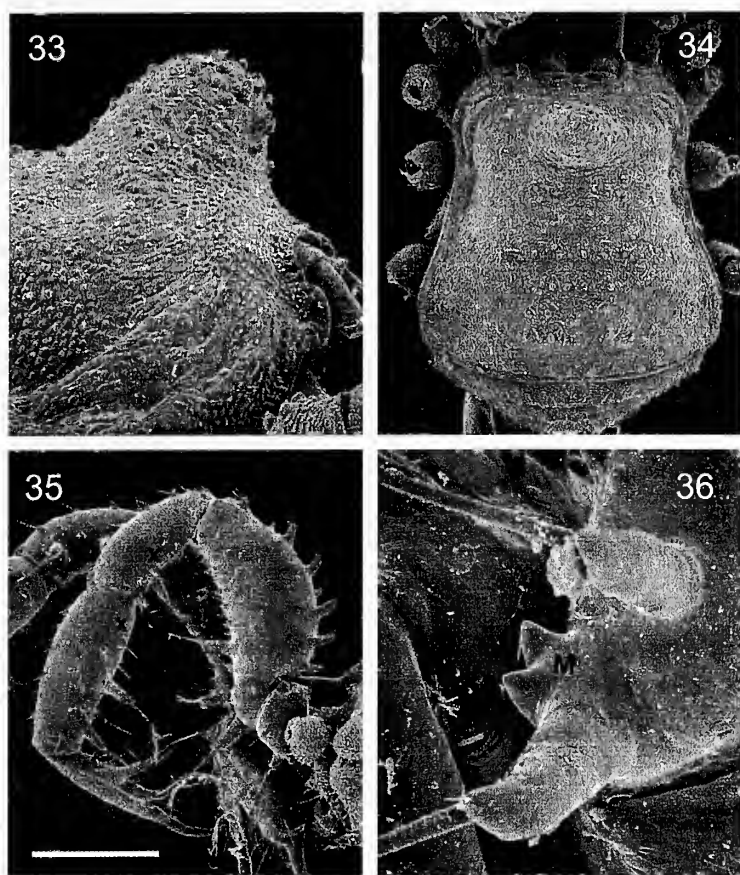
Penis (Figs. 37–40): VPP curved inward, with maximum separation greater than prong width; AS distally curved, as long as longest VPP setae; with 10 long setae on each prong.

Glans with apical styler region consisting of triangular pointed stylus and a pair of curved, apically pointed PSL.

Female (paratype): Total body length, 1.54. Scute length, 1.00; width, 0.91. Eyemound length, 1.54. Scute length, 1.00; width, 0.91. Eyemound length, 0.27; width, 0.32; height, 0.18. Leg II length, 6.45. Leg II/Scute length, 6.45.

Ovipositor not expanded due to the fragile condition of the single known female specimen.

Sexual dimorphism.—Male with enlarged or double mesal tubercle at base of proximal megaspine of palpal femur; tubercles absent in female. The palpal patellar ectal and tibial



Figures 33–36.—*Banksula tutankhamen*, male. 33, anterior of scute, lateral view, with eyemound showing absence of cornea; 34, dorsal view of body; 35, lateral view of left palp showing reduced ectal megaspines on patella and tibia (X); 36, ventrobasal view of left palpal femur showing absence of ectal end presence of double mesal tubercle (M) at ventral megaspine. Scale bar: 33 = 150 μm ; 34, 35 = 430 μm ; 36 = 75 μm .

ectobasal megaspines are shorter in males, being at most 1/2 the length of those in females.

Juveniles.—The single juvenile collected with the adults is an early instar with depigmented and smooth integument; chelicerae lacking ectobasal knob; with gray retina and small cornea present; palpal megaspines as in adult except that tibia has 1 ectal and 2 mesal megaspines, and base of femur without mesal or ectal tubercle; tarsi III and IV with 2 claws and small arolium; TC, 1–1–2–2.

Remarks.—Collected from the steep inner chamber of the dark zone of King Tut Cave in the Calaveras Limestone.

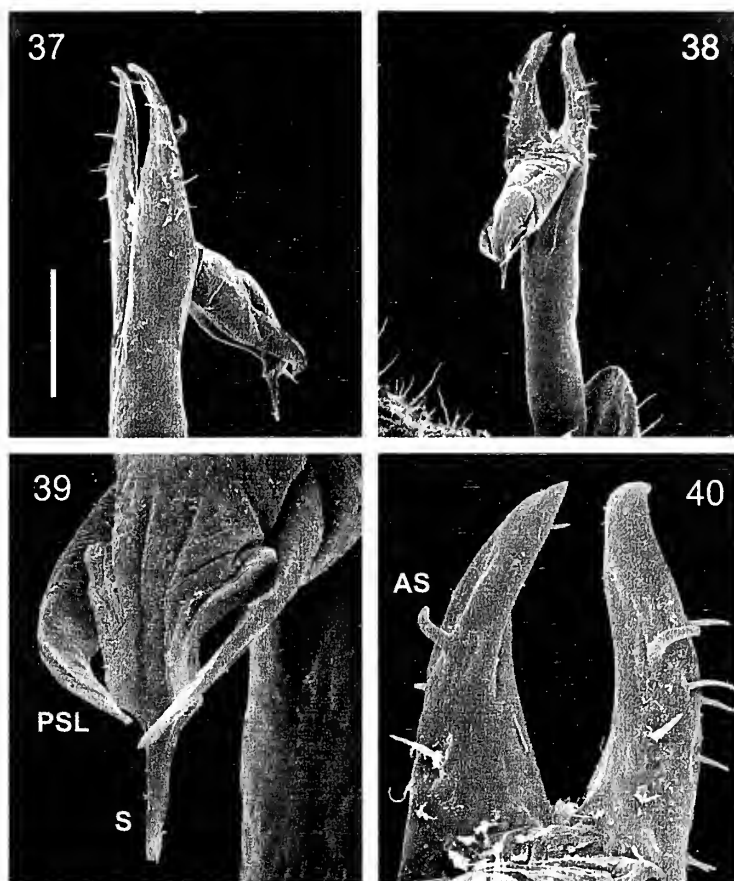
Material examined.—All from the type locality: 2♂, 1 ♀, 1 juvenile (same data as holotype), CAS.

Distribution.—Known only from King Tut Cave, Calaveras County, California.

Banksula martinorum Briggs & Ubick
Figs. 9, 41–45

Banksula martinorum Briggs & Ubick 1981:318.

Diagnosis.—This species differs from oth-



Figures 37–40.—*Banksula tutankhamen*, penis. 37, lateral view; 38, dorsal view; 39, close-up of glans showing stylus (S) and parastylar lobes (PSL); 40, dorsal view of ventral plate prongs showing curved apical spines (AS). Scale bar: 37 = 100 μm ; 38 = 150 μm ; 39 = 30 μm ; 40 = 43 μm .

ers in the *californica* group by the presence of a thick blunt AS on the penis and the absence of an ectal tubercle at the proximal megaspine of the palpal femur in females.

Additional description.—Eyemound H/L 0.68; eye with degenerate retina and cornea.

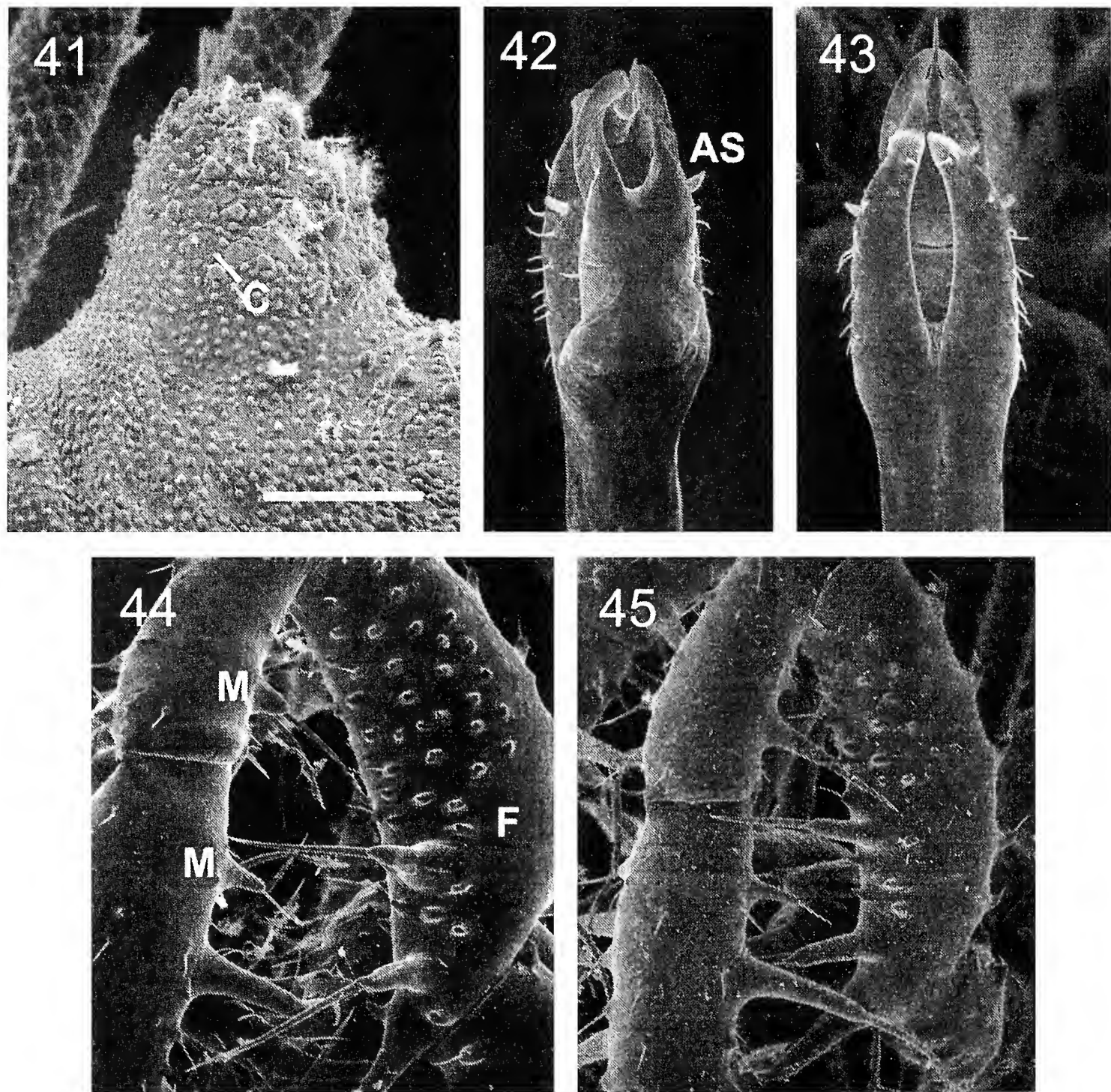
Male: Proximal megaspine of palpal femur with mesal and ectal tubercles at base; palpal patellar ectal megaspine 1/2 length or less than the corresponding spine in females. Penis: AS truncate; AS/VPW ratio 0.5; VPP with 11 long setae. Distal separation of VPP less than prong width.

Female: Proximal megaspine of palpal femur lacking tubercles at base.

Material examined.—All 15 known specimens.

New record.—Calaveras County: Heater Cave, 8 km N Columbia, 6♂, 2♀, 2 juveniles (15 Oct. 1994, T. Briggs, W. C. Rauscher, D. Ubick).

Distribution.—Known only from Heater Cave, 8 km N Columbia, Calaveras County, California.



Figures 41–45.—*Banksula martinorum*. 41, eyemound of female showing degenerate cornea (C), anterior to left; 42, dorsal view of penis showing thick apical spine (AS); 43, ventral view of penis; 44, left male palp, ectal view, showing enlarged femur (F) and reduced ectal megaspines (M) on patella and tibia; 45, left female palp, ectal view, showing unmodified femur and ectal megaspines on patella and tibia. Scale bar: 41–43 = 100 μ m; 44, 45 = 250 μ m.

Banksula tuolumne Briggs
Figs. 9, 46–49

Banksula tuolumne Briggs 1974: 5; Briggs & Ubick 1981: 316.

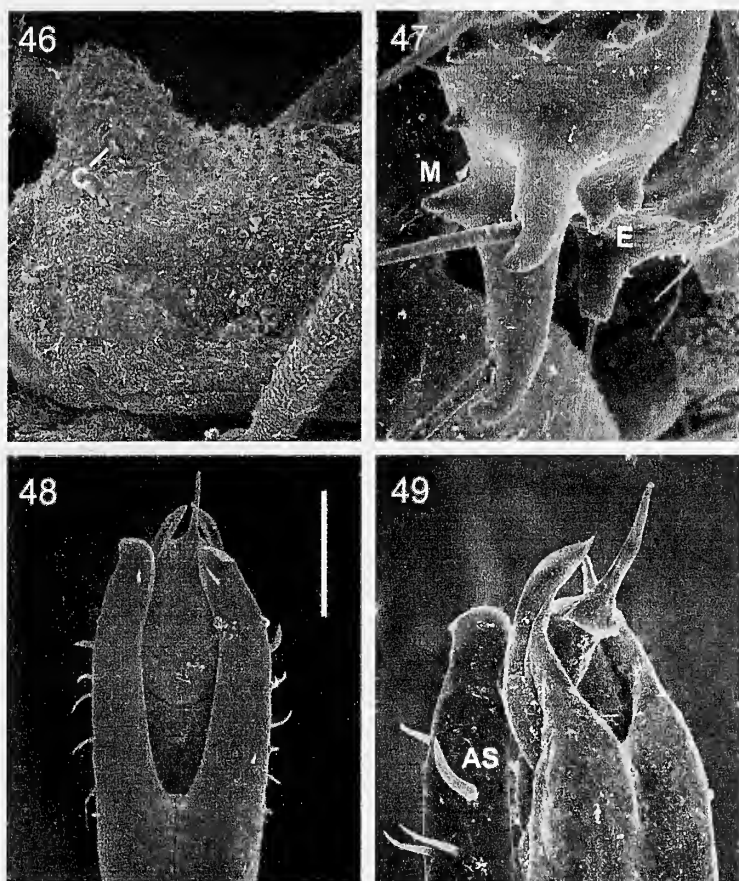
Diagnosis.—This species differs from others in the *californica* group by the presence of a rounded double ectal tubercle at the base of the proximal megaspine on the palpal femur in males and the reduced proximal ectal megaspine of the palpal tibia in females.

Additional description.—Eyemound H/L 0.69; eye with degenerate retina and cornea.

Proximal ectal megaspine on palpal tibia less than 1/2 length of distal ectal one.

Male: Proximal megaspine of palpal femur with robust mesal and rounded double ectal tubercles at base; palpal patellar ectobasal megaspine 1/2 length or less than the corresponding spines in females. Penis: AS/VPW ratio 0.7; VPP with 7–9 long setae. Distal separation of VPP equal to or wider than prong width.

Female: Palpal tibia with reduced ectal proximal megaspine; proximal megaspine of



Figures 46–49.—*Banksula tuolumne*, male. 46, anterior of scute with eyemound showing cornea (C); 47, ventrobasal portion of palpal femur showing mesal tubercle (M) and double ectal tubercle (E) at ventrobasal megaspine; 48, ventral view of penis; 49, dorsolateral view of penis showing curved apical spine (AS). Scale bar: 46 = 250 μ m; 47 = 100 μ m; 48 = 75 μ m; 49 = 43 μ m.

femur with acute ectal tubercle and lacking mesal tubercle at base.

Material examined.—All 18 known specimens.

New record.—Tuolumne County: Tuolumne Crystal Cave, 8 mi SE Tuolumne, 2♂, 4 ♀, 1 juvenile (16 Jun. 1979, D. Cowan, J. Espinal).

Distribution.—Known only from Tuolumne Crystal Cave, near Tuolumne, Tuolumne County, California.

The *melones* species group

Diagnosis.—Members of this species group are distinguished from *B. incredula* in having a relatively lower TC of 4–6–5–6 and a palpal femur with only 3 ventrobasal and 1 mesoapical megaspines. They differ from members of the *californica* group in having a larger GO, with a GO/S width ratio of 0.3 as opposed to 0.2 (Fig. 8), and in lacking sexually dimorphic palpi.

Included species.—*B. grahami* and *B. melones*.

Remarks.—These two species, in contrast to those of the *californica* group, have distinctive genitalia, and are the only species in the genus with a broadly parapatric distribution. Also unique in the *melones* group, until just a couple of decades ago, was the presence of sympatry in *Banksula* species. *Banksula melones* and *B. grahami* both occurred in Mclean's Cave until it was flooded by the damming of the Stanislaus River. Prior to the flooding, individuals of both species, along with about 30 other cavernicole species, were transplanted to a nearby limestone mine (Transplant Mine) in 1975 and again in 1978 (Elliott 1978). About 90 individuals of *B. melones* and over 200 of *B. grahami* were transplanted. When we visited the Transplant Mine in 1986 it appeared that one species had become extinct as we encountered only a thriving population (50 individuals) of the larger species, *B. melones* (Briggs 1987). And more recently, in 1996, even that species seems to be on the decline as we observed only six individuals.

Distribution.—Known only from caves and mines in the Sierran Motherlode Region along the Stanislaus River in Calaveras to Tuolumne Counties, California.

Banksula melones Briggs

Figs. 8, 9, 50–57

Banksula melones Briggs 1974: 8; Briggs, 1987: 12; Briggs & Ubick 1981: 320; Elliott 1978: 6.

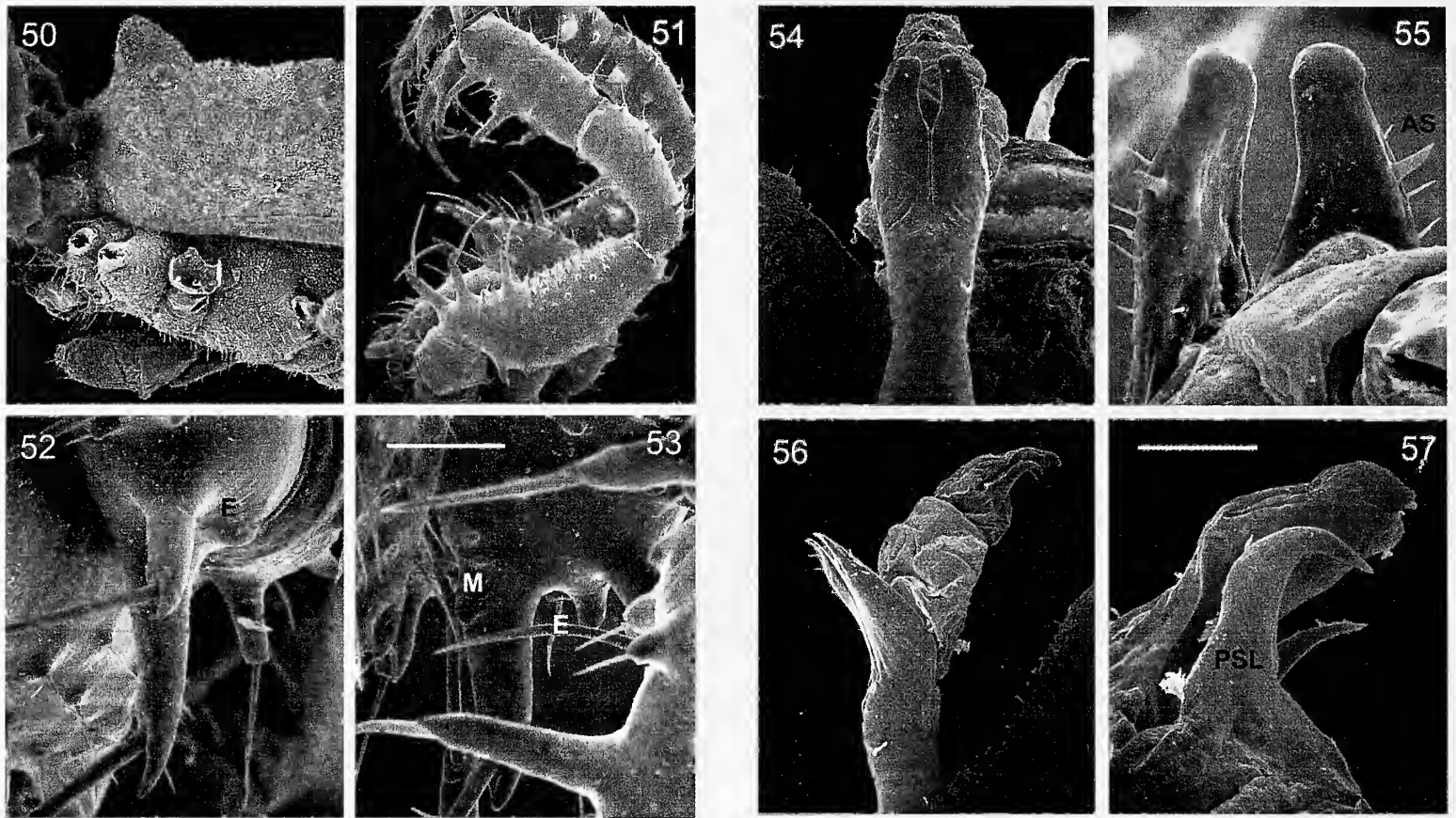
Diagnosis.—This species differs from *B. grahami* in having a larger body size, well developed eyes, and pointed PSL on the glans penis.

Additional description.—Male: Proximal megaspine of palpal femur with mesal and large ectal tubercles basally. Penis: VPP broad with narrow separation, less than 0.5 prong width; AS straight, pointed, and of moderate length, about 0.5 prong width; with 9 setae, slightly shorter than AS, on each prong. Glans with broad rounded stylus and curved pointed PSL.

Female: Proximal megaspine of palpal femur with rounded ectal tubercle, lacking mesal tubercle. Ovipositor with sparsely microspined cuticle; without AT at apex.

Material examined.—All 145 known specimens.

New records.—Tuolumne County: McLean's Cave, 4.5 km N Columbia, 3 ♂, 2 ♀



Figures 50–53.—*Banksula melones*, female from McLeans Cave (50–52), male from Lost Piton Cave (53). 50, anterior half of body; 51, lateral view of palpi; 52, ventrobasal part of left palpal femur showing ectal tubercle (E) of ventrobasal megaspine; 53, ventrobasal part of left palpal femur showing ectal (E) and mesal (M) tubercles of ventrobasal megaspine. Scale bar: 50, 51 = 430 μm ; 52, 53 = 100 μm .

(5 Mar. 1981, G. Hunter, D. Kavanaugh, D. Ubick); Transplant Mine, 3 km N Columbia, 9 δ , 5 ϕ (11 Jun. 1982, T. Briggs); 1 ϕ (6 Dec. 1986, T. Briggs, V. Lee, D. Ubick).

Distribution.—Known from caves, and one population transplanted to a mine (Briggs 1987; Elliott 1978), along the Stanislaus River in Calaveras and Tuolumne Counties, California.

Banksula grahami Briggs

Figs. 9, 58–66

Banksula grahami Briggs 1974: 7; Briggs 1987: 12; Briggs & Ubick 1981: 320; Elliott 1978: 6.

Banksula elliotti Briggs & Ubick 1981: 319. New synonymy.

Diagnosis.—This species differs from *B. melones* in having a smaller body size, at least somewhat reduced eyes, and rounded PSL on the glans penis.

Additional description.—Eye with cornea and retina small to vestigial to absent. Proximal megaspine of palpal femur with curved ectal tubercle basally.

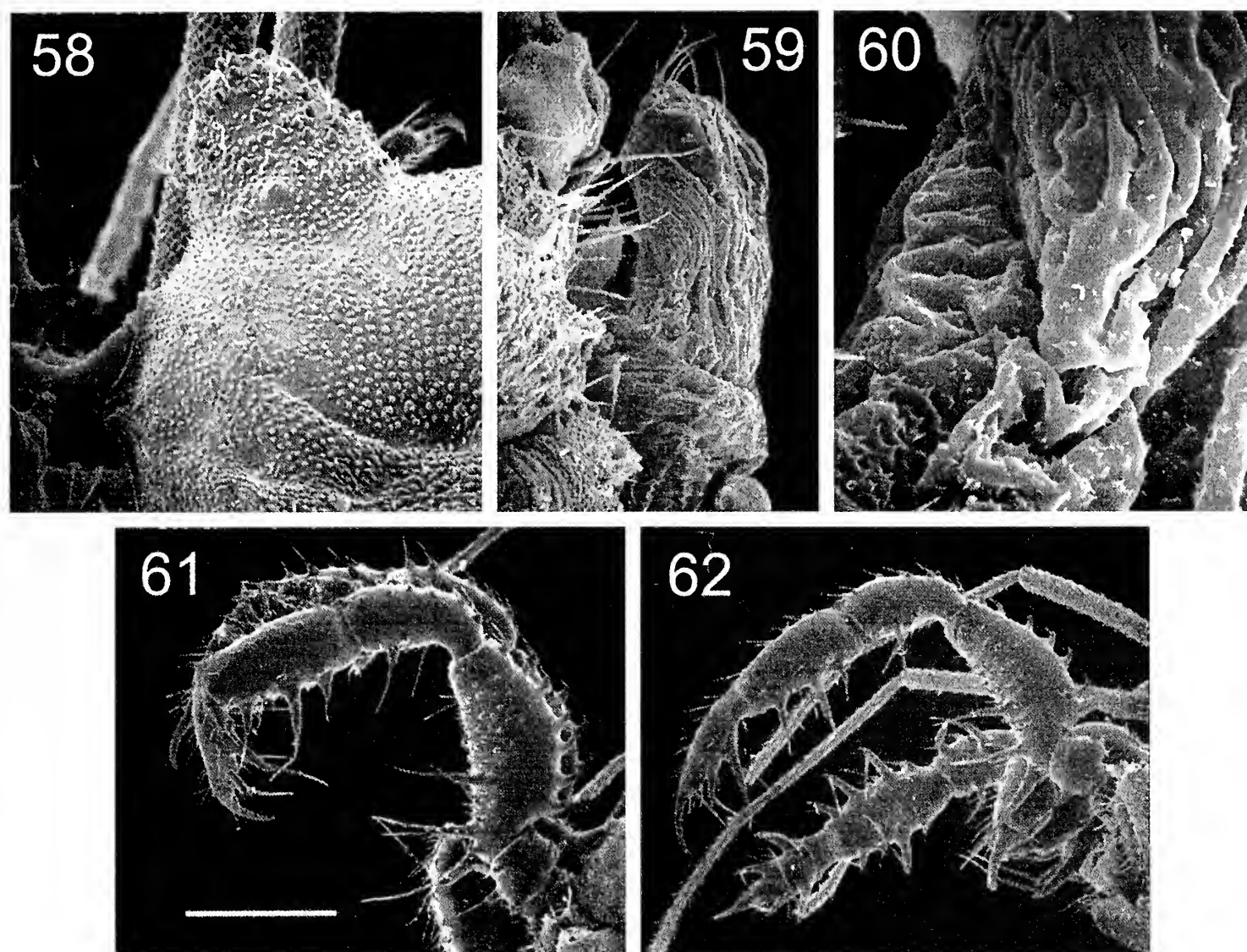
Figures 54–57.—*Banksula melones*, male from Lost Piton Cave. 54, ventral view of penis; 55, dorsal view of ventral plate showing stout apical spines (AS); 56, lateral view of penis showing expanded glans; 57, close-up of glans tip showing wide stylus and hook-like parastylar lobes (PSL). Scale bar: 54, 56 = 200 μm ; 55 = 60 μm ; 57 = 43 μm .

Male: Palpal femur with mesal tubercle at base of proximal megaspine. Penis: VPP broad with narrow separation, from less than 0.5 to 0.2 prong width; AS straight and very short, about 0.2 prong width; with about 9 setae, subequal to AS length. Glans with broad rounded stylus and curved apically rounded PSL.

Female: Ovipositor with densely microspined cuticle; without AT at apex.

Variation: About 20% of the females have a small mesal tubercle at the basal megaspine on one or both palpi.

Remarks.—The diagnostic character for recognizing *B. elliotti*, the absence of eyes, does not stand up to close scrutiny. Although the majority of specimens from the northeastern most locality (Pinnacle Point Cave) show no trace of eyes, those at *elliotti*'s southern end (Rabbit Hole, Grapevine Gulch, and Digger Pine Caves) show degenerate although clearly vestigial eyes, similar to the condition in some *grahami* populations (*Banksula* Cave). There appears to be a clinal variation taking place with the general trend of increas-



Figures 58–62.—*Banksula grahami*, male from Crystal Palace Cave (58, 61), female from Banksula Cave (59, 60, 61). 58, lateral view of anterior half of scute; 59, lateral view of ovipositor; 60, close-up of ovipositor showing microspines; 61, 62, lateral view of palpi. Scale bar: 58 = 180 μm ; 59 = 150 μm ; 60 = 30 μm ; 61 = 430 μm ; 62 = 530 μm .

ing troglomorphy from the SW part of the *grahami* distribution (Moaning to Carlow's Cave) to the NE sector (Pinnacle Point Cave). Similar clinal variation has been recorded for *Texella*, especially *T. reddelli* and *T. reyesi* (Ubick & Briggs 1992).

Material examined.—All 152 known specimens.

New record.—Tuolumne County: McLean's Cave, 4.5 km N Columbia, 3 ♂, 2 ♀ (5 Mar. 1981, G. Hunter, D. Kavanaugh, D. Ubick).

Distribution.—Known from caves and mines along the Stanislaus River in Calaveras and Tuolumne Counties, California.

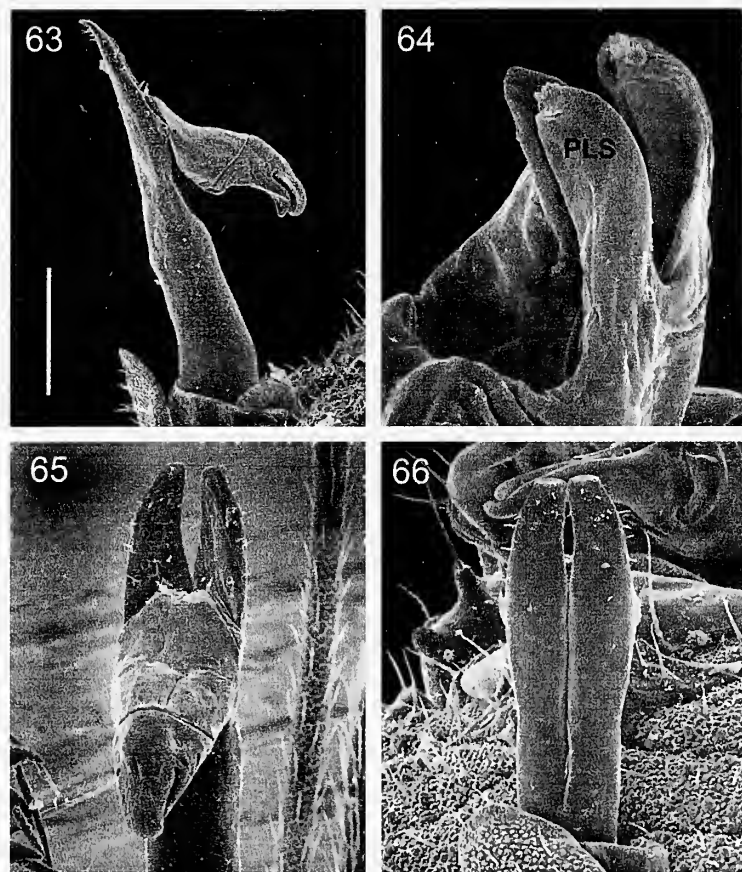
PHYLOGENY

The relationship of *B. incredula* to other *Banksula* was examined using outgroup comparison. *Calicina mariposa* (Briggs) and *Sitalcina californica* (Banks) were used as examples of taxa with unmodified (entire)

ventral plates. For the genera with bifurcate ventral plates, the "bifurcate complex", we used *Texella bifurcata* (Briggs) and a *Crosbyella* species, the latter to represent the eastern Nearctic genera. We found 18 characters useful in inferring relationships within *Banksula* and to other Phalangodidae. These are presented in tabular form in Table 1 and elaborated below.

Character 1. Glans type. Of the two types of glans construction in Phalangodidae, the folding glans is found in the vast majority of species. This is believed to be the derived condition based on its greater complexity and is a synapomorphy for all Nearctic genera except *Calicina* (Ubick & Briggs 1989).

Character 2. Ventral plate type. An unmodified, or entire, ventral plate is found in most western Nearctic and all Palearctic phalangodids. The ventrally incised, or bifurcate, condition is considered derived and a synapomorphy for *Banksula*, *Texella*, and all eastern



Figures 63–66.—*Banksula grahami*, male from Crystal Palace Cave. 63, lateral view of penis; 64, ventroapical view of glans showing rounded parastylar lobes (PSL); 65, dorsal view of penis; 66, ventral view of penis. Scale bar: 63 = 200 μm ; 64 = 43 μm ; 65, 66 = 150 μm .

Nearctic phalangodids (Ubick & Briggs 1992).

Character 3. Ventral plate position. In *Banksula* the ventral plate prongs are ventrally positioned, as they are in the unmodified (entire) ventral plate. The lateral placement of the VPP is thus as an apparent synapomorphy for *Texella* and the eastern genera (Ubick & Briggs 1992).

Character 4. Ventral plate with apical spine. An inarticulate apical spine is present on the ventral plate prongs of all *Banksula* and *Texella* species but has not yet been discovered, even in vestigial form, in the eastern taxa. This character contradicts the grouping by the previous one by appearing to be a synapomorphy for *Banksula* and *Texella* (Ubick & Briggs 1992).

Character 5. Palpal femur with setiferous dorsal tubercles. These tubercles are not known from other phalangodids apart from *Banksula* (Figs. 2, 3), although similar but asetose tubercles may occur in some species of *Sitalcina* (Figs. 4, 5).

Character 6. Ovipositor with apical teeth. A pair of apical teeth occurs on the ovipositor

of *B. incredula* (Fig. 15) and most *Texella* species, including *T. bifurcata* (Ubick & Briggs 1992: fig. 19). The presence of these teeth in *B. incredula* is interpreted as a plesiomorphic retention and their absence a synapomorphy for the remaining *Banksula*.

Character 7. Ventral plate setal length. In *T. bifurcata* and most other species of *Texella* the setae on the ventral plate are long, at least as long as the width of a ventral plate prong (Ubick & Briggs 1992: fig. 15). In *B. incredula*, the setae are about equal to the VPP width (Fig. 20), in the *B. californica* group, the setae are about one-half VPP width (Fig. 24), and in the *B. melones* group they are about one-third or less (Fig. 55). Reduction in size of ventral plate setae in *Banksula* appears to be derived.

Character 8. Meso-apical megaspines of palpal femur. *B. incredula* has 2 meso-apical megaspines on the palpal femur (Fig. 11), whereas other *Banksula* have only one. The former appears to be the generalized condition, perhaps another synapomorphy for the bifurcate complex of genera, and is found in most species of *Texella* and the eastern genera. The loss of one meso-apical megaspine is thus synapomorphic for the remaining *Banksula* species.

The above three characters are plesiomorphic retentions in *B. incredula*. In addition to these we have identified six characters that appear to be autapomorphies for *B. incredula*, further attesting to its uniqueness and arguing for its placement in a separate species group:

Character 9. Ovipositor cuticle texture. *B. incredula* females have a smooth ovipositor surface (Fig. 17), in contrast to the spiny cuticle of other *Banksula* (Fig. 27, 60), *Texella* (Ubick & Briggs 1992: fig. 21), *Sitalcina* (Ubick & Briggs 1989: fig. 1d), and *Calicina* (Ubick & Briggs 1989: fig. 5).

Character 10. Ventral megaspines on palpal femur. The presence of four ventrobasal megaspines on the palpal femur in *B. incredula* (Fig. 12, 13), is unique in the Nearctic phalangodids that have only three (as in *T. bifurcata* in Ubick & Briggs 1992: fig. 21).

Character 11. Eyemound height. *B. incredula* has a high pointed eyemound (Fig. 10). Measured as a ratio of height/length, the eyemound in *B. incredula* (1.0) is greater than in other *Banksula* (0.6–0.8), *T. bifurcata* (0.7),

Table 1.—Character matrix for *Banksula* species groups and selected Nearctic phalangodid genera. Bold character states are derived. (See text for explanation.)

	<i>Calicina</i> <i>mariposa</i>	<i>Sitalcina</i> <i>californica</i>	<i>Banksula</i> <i>incredula</i>	<i>Banksula</i> <i>californica</i>	<i>Banksula</i> <i>melones</i>	<i>Texella</i> <i>bifurcata</i>	<i>Crosbyella</i> sp.
1.—glans type	telescoping	folding	folding	folding	folding	folding	folding
2.—ventral plate	entire	entire	bifurcate	bifurcate	bifurcate	bifurcate	bifurcate
3.—vp position	ventral	ventral	ventral	ventral	ventral	lateral	lateral
4.—vp w/as	no	no	yes	yes	yes	yes	no
5.—p fm w tubs	no	no	yes	yes	yes	no	no
6.—ovip w at	no	no	yes	no	no	yes	no
7.—vp setal length	short	short/long	long	short	very short	long	short
8.—mes mgsp p fm	1—	2—	2—	1—	1—	2—	2—
9.—ovip cuticle	spiny	spiny	smooth	spiny	spiny	spiny	?
10.—vent mgsp p fm	3—	3—	4—	3—	3—	3—	3—
11.—eyemound h/l	<1	1—	1—	<1	<1	<1	<1
12.—leg II/scute	2.4—	2.6—	4.6–5.6	4.2–5.2(–6.4)	3.6–4.7	2.6–3.3	3.4—
13.—tarsal count	3–5–5–5	3–5–5–5	>4–6–5–6	4–6–5–6	4–6–5–6	<3–5–5–5	4–6–5–6
14.—body length	<1.5	1.5–2.5	>2.5	1.5–2.5	1.5–2.5	1.5–2.5	>2.5
15.—m p fm	normal	normal	normal	enlarged	normal	normal	normal
16.—ect mgsp m p	normal	normal	normal	reduced	normal	normal	normal
17.—go/scute w	0.2—	0.2—	0.2—	0.2—	0.3—	0.2—	0.2—
18.—stylus width	thin	thin	thin	thin	fat	thin	thin

and most other nearctic phalangodids (except *Sitalcina californica*, but not other *Sitalcina*).

Character 12. Leg II/scute length. The relative leg length (measured as Leg II length/Scute length) of *B. incredula* (4.6–5.6) is greater than that of *C. mariposa* (2.4), *S. californica* (2.6), *T. bifurcata* (2.6–3.3), and *Crosbyella* (3.4). It is also greater than or as large as most species of *Banksula* (3.6–5.2), except that of *B. tutankhamen* (6.0–6.4).

Character 13. Tarsal count. The tarsal count in *B. incredula* varies from 4–7–5–6 to 5–9–5–6 and is greater than in other *Banksula* species, where it is a constant 4–6–5–6. It is also higher than in *Calicina mariposa* (3–5–5–5), *Sitalcina* (3–5–5–5), *Crosbyella* (4–6–5–6), and the basal species of *Texella* (3–5–4–5).

Character 14. Body length. The body length of *B. incredula* (2.6–3.0 mm) is significantly larger than that of other *Banksula* (1.5–2.2), *C. mariposa* (1.4–1.5), *S. californica* (1.4–1.9), *T. kokoweef* (1.7–1.8) and *T. bifurcata* (1.5–2.1), but is subequal to that of *Crosbyella* species.

The above three characters seem to be linked. Certainly in troglobitic opilionids both leg hypertrophy and increased tarsal counts are strongly correlated. Hypertrophy of legs and other appendages is a common occurrence in cavernicole animals. In our studies of phalangodids, we have examined numerous instances of this phenomenon in *Calicina* (Ubick & Briggs 1989), *Texella* (Ubick & Briggs 1992), and *Sitalcina* (Briggs 1968). In all instances, we found that the appendages of cavernicole species (or populations) are relatively longer than those of their epigean counterparts and in troglobitic forms, longer than those of their troglophilic relatives. In *B. incredula* we now have an interesting example of a leg hypertrophy that is not a consequence of troglomorphy and which, therefore, requires a different explanation. Even were we to allow that the species' talus habitat is sufficiently cave-like, the harvestman is nonetheless endowed with well-developed eyes and dark pigmentation. A more plausible scenario, however, is that this is an example of allometric growth and that the increased appendage length and tarsal count is a consequence of greater body size.

Character 15. Male palpal femur. In the *Banksula californica* species group, but not in

other *Banksula*, the male palpal femur is enlarged, being thicker than the female's.

Character 16. Ectal megaspines on male palp. Also unique to the *B. californica* group is a sexual dimorphism in which males have reduced mesal megaspines on the palpal patella and tibia (Fig. 44, 45).

Character 17. Genital operculum size. The *B. melones* group is most readily defined on the basis of its enlarged genitalia. Measured in terms of the relative size of the genital operculum, the GO/S width is about 0.3 in the *melones* group (Fig. 8), but only 0.2 in the *incredula* (Fig. 6) and *californica* groups (Fig. 7).

Character 18. Stylus width. In most phalangodids the stylus is slender, except for the *B. melones* group where it is very broad (Figs. 57, 64).

Our interpretation of these characters place the *melones* and *californica* groups as sisters and derived relative to the *incredula* group. The position of *Banksula* within the bifurcate complex is not yet resolved due to character discordance but, because of its relatively simple glans and ventrally positioned VPP, the genus is most probably basal within the complex.

The relationships of the species groups are presented as an area cladogram (Fig. 9). *Banksula* is endemic to California with the most derived groups restricted to the Sierra Nevada and the basal *incredula* group currently known from a single coastal locality. Upon examining the distributions, an immediate difference between the two Sierran groups becomes apparent. The seven species of the *californica* group are spread across a wide area of territory and each species is known from a single isolated cave. By contrast, the two species of the *melones* group, which exhibit a parapatric boundary, are known from a total of over 30 caves, all clustered in a small area.

As mentioned earlier, species in the *californica* group show little variation of the male reproductive structures. Although there are differences in the VPP placement and armature among these species, their glans morphology is remarkably uniform (compare Figs. 24, 29, 38, 43). In the *melones* group, however, the two species are readily recognized by the form of the glans (Figs. 57, 64). Why this difference? This may well be an example, on one hand, of morphological con-

stancy in consequence of isolation and, on the other, of genitalic divergence in consequence of close proximity. We have encountered a similar trend in *Texella*, with the genitalic homogeneity of the isolated troglobitic species of the *mulaiki* group (Ubick & Briggs 1992, figs. 85–108) compared to the genitalic exuberance of the largely epigeal *spinoperca* group (figs. 168–200).

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SHORT COMMUNICATION

THE FIRST RECORD OF AMBLYPYGI FROM EGYPT

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ABSTRACT. *Charinus ioanniticus* (Kritscher 1959) (Charinidae) is recorded for the first time from Egypt. Two specimens were collected from Burg El-Arab near the Mediterranean coast, north of Egypt.

Keywords: Amblypygi, *Charinus ioanniticus*, Egypt

Amblypygi are widely distributed throughout the tropics and subtropics but most genera have a localized distribution. The sole exception is *Charinus* Simon 1892 which is circum-tropical (Weygoldt 2000). The amblypygid fauna of the eastern Medi-

terranean region is represented by *Charinus ioanniticus* (Kritscher 1959) which has been reported from Greece, Israel and Turkey (Kritscher 1959; Kraus 1961; Weygoldt 1972; Kovařík & Vlasta 1996). Among an arthropod collection from the

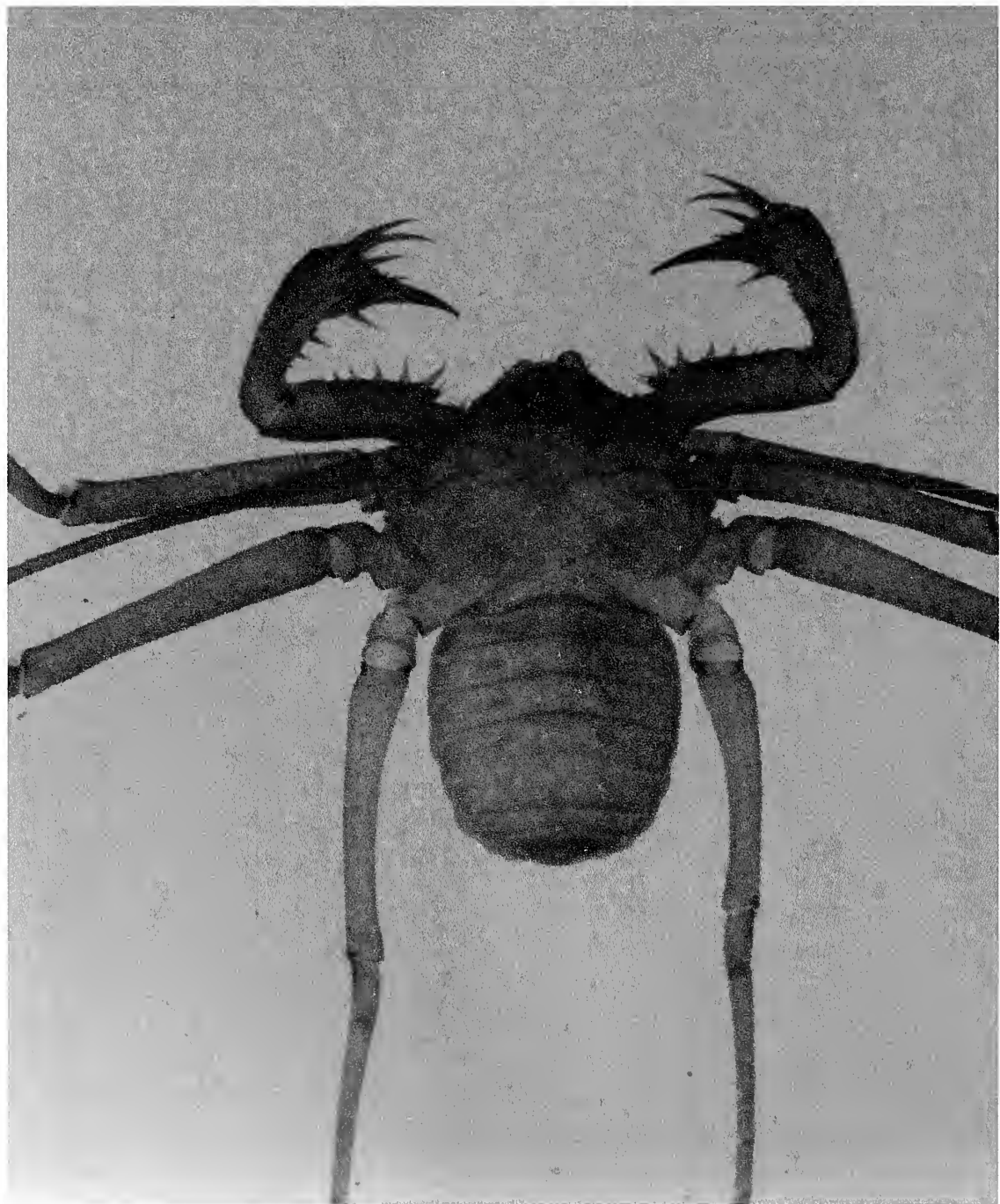


Figure 1.—Dorsal view of *Charinus ioanniticus* female, from El-Mallahat near Burg El-Arab, Egypt.



Figure 2.—Distribution map of *Charinus ioanniticus* in the eastern Mediterranean region. Solid circles represent recorded localities, clockwise from top: Kos, Rhodes, Samanda (Seleucia), Nazareth, Jerusalem, and Burg El-Arab.

western area of the Mediterranean coast of Egypt made by Drs. A. H. Ali and T. Tantawi on the Faculty of Science of Alexandria University, I found two females of *C. ioanniticus* collected about 50 km west of Alexandria. These specimens represent the first record of Amblypygi from Egypt.

Charinus ioanniticus (Kritscher 1959)

Figs. 1 & 2

Lindosiella ioannitica Kritscher 1959: 454–457; Kraus 1961: 491. *Charinus ioanniticus* (Kritscher): Weygoldt 1972: 123, 129; Delle Cave 1986: 163; Kovařík & Vlasta 1996: 57–58; Weygoldt 2000: 74, 126.

Material examined.—**EGYPT:** El-Mallahat near Burg El-Arab, 2 females, 19 September 1998, Drs. A. H. Ali and T. Tantawi, in the author's collection.

Remarks.—My subsequent visit to the area (30°55'36"N, 29°31'50"E, elevation 20m) on 8 October 2000, in which I inspected the ruins of an old stony building with a deep rectangular room in the middle, identical to the description of Dr. Ali, failed to locate any further specimens.

The specimens listed here fit the previous descriptions of *C. ioanniticus* (e.g. Kritscher 1959; Weygoldt 1972), and the larger specimen (Fig. 1) has the following measurements (in mm): total length 7.56; prosoma length 2.97; width 4.25, width/length 1.43; opisthosoma length 4.59.

Like many other species of *Charinus*, *C. ioanniticus* appear to prefer a saxicolous habitat. Kritscher (1959) described a new genus and new

species *Lindosiella ioannitica* from Lindus in Rhodes, Greece. A male, three females and four juveniles were found in crevices of walls and rocks in April. Previous records of *Charinus ioanniticus* and this new discovery in North Africa, show that this taxon is distributed around the eastern Mediterranean (Fig. 2). It is expected that careful searching will reveal further localities in this area.

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Cover photo: Threatening display of an adult male *Acanthoscurria suina* (Theraphosidae) from Uruguay. Photo by Antonio Mignone, Montivideo, Uruguay.

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LINYPHIA TRIANGULARIS, A PALEARCTIC SPIDER (ARANEAE, LINYPHIIDAE) NEW TO NORTH AMERICA

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ABSTRACT. A Palearctic spider, *Linyphia triangularis* (Clerck 1757), has been accidentally introduced to the U.S.A. and populations successfully established in Maine. The date, origin, and focal point(s) of introduction are unknown, but suspected to be recent, European, and maritime. Extensive historical collections, records of maritime commerce, and recent chronological collections support this hypothesis. Results of cursory surveys in 1999 and 2000 indicate that *L. triangularis* is now widely distributed in Maine with specimens taken in 15 of 16 counties. The potential impact(s) of *L. triangularis* on the native araneofauna are unknown, but possibly detrimental. In Europe, this species exhibits aggressive behaviors (e.g., web “take-overs”) toward conspecifics and congenetics.

Keywords: Introduced species, Maine spiders, aggressive linyphiid, recent invasions

Spiders are dispersed over great distances by aerial ballooning and by human transport (Gertsch 1979; Kaston 1983). Several species have been implicated as immigrants to North America from Europe and elsewhere; common examples include *Araneus diadematus* Clerck 1757, *Salticus scenicus* (Clerck 1757), *Pholcus phalangioides* (Fuesslin 1775), *Achaeearanea tepidariorum* (C.L. Koch 1841), *Tegenaria domestica* (Clerck 1757), and *Dysdera crocata* C.L. Koch 1838 (Gertsch 1979). More recently, the northeastern United States and Canada have seen introductions of *Steatoda bipunctata* (Linnaeus 1758) from Europe (Nyffeler et al. 1986), and of *Achaeearanea tabulata* Levi 1980, possibly from Asia (Dondale et al. 1994). In California, Griswold & Ubick (2001) noted the introduction of *Zoropsis spinimana* (Dufour 1820), a native to the Mediterranean region. Here we describe the invasion and establishment of yet another exotic spider in North America, i.e., *Linyphia*

triangularis (Clerck 1757), which presumably is an immigrant from Europe.

Chronology of discovery.—During 1991, 1996, and 1997, F. G., Jr. collected female linyphiid spiders in old field vegetation at Milbridge, Washington County, Maine. Subsequently, D. T. J. determined the specimens to be *Linyphia triangularis* (Clerck 1757), a Palearctic spider. Peter J. van Helsdingen of the National Museum of Natural History in Leiden confirmed the species identity.

The abundance of *Linyphia triangularis* in Maine became evident when 9 males, 20 females, and 2 juveniles were readily taken on 19 August 1998 at Schoodic Peninsula, Acadia National Park, Winter Harbor, Hancock County. Our suspicion that *Linyphia triangularis* had successfully established a breeding population at Schoodic Peninsula was confirmed on 19 August 1999, when 5 males and 18 females were taken in < 2 h at the same site sampled in 1998. Most were found in slightly dome-shaped webs on understory forbs (*Solidago* sp.), grasses, ferns, and shrubs near the ground; a few were taken by beating and sweeping lower-crown foliage of red spruce, *Picea rubens* Sargent, and by search-

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ing loose bark and tree boles of paper birch, *Betula papyrifera* Marshall.

Males and females were observed cohabitating in the same web; however, mating and oviposition were not observed either year.

Associated species of sheet-line weavers (Linyphiinae) at Schoodic included: adults of *Bathyphantes pallidus* (Banks 1892), *Centromerus denticulatus* (Emerton 1909), *Drapetisca alteranda* Chamberlin 1909, *Helophora insignis* (Blackwall 1841), *Lepthyphantes calcaratus* (Emerton 1909), *L. turbatrix* (O.P.-Cambridge 1877), *Microneta viaria* (Blackwall 1841), *Nerienne radiata* (Walckenaer 1841), and *Tapinopa bilineata* Banks 1893; and juveniles of *Frontinella*, *Helophora*, *Nerienne*, and *Pityohyphantes*. Based on collection frequency, none of the associated adult linyphiids ($n = 18$) was as common as *Linyphia triangularis* in 1998; none of associated adult or juvenile linyphiids ($n = 19$) was as common as *L. triangularis* in 1999.

Prior collections.—None of the contacted museums or institutions had records of *L. triangularis* collected in Maine or elsewhere in North America. These included: The American Museum of Natural History (AMNH), New York; California Academy of Sciences (CAS), San Francisco; Canadian National Collection (CNC), Ottawa; Field Museum of Natural History (FMNH), Chicago; Harvard Museum of Natural History (HMNH), Cambridge; Thomas Burke Museum (TBM), Seattle; and, U. S. National Museum of Natural History (NMNH), Washington.

Procter (1946) listed 15 families, 94 genera, and 179 species of spiders collected from various habitats on Mount Desert Island, Hancock County, Maine. *Linyphia triangularis* was not among them.

Examination of D. T. J.'s undetermined material yielded 7 males and 10 females of *L. triangularis* collected during August of 1983, 1986, 1989, and 1994, and from the counties of Cumberland, Hancock, Penobscot, and York (Map 1). The earliest record of *L. triangularis* in Maine is a female taken 28 August 1983 at Stover Corner, Brooksville, Hancock County, Maine.

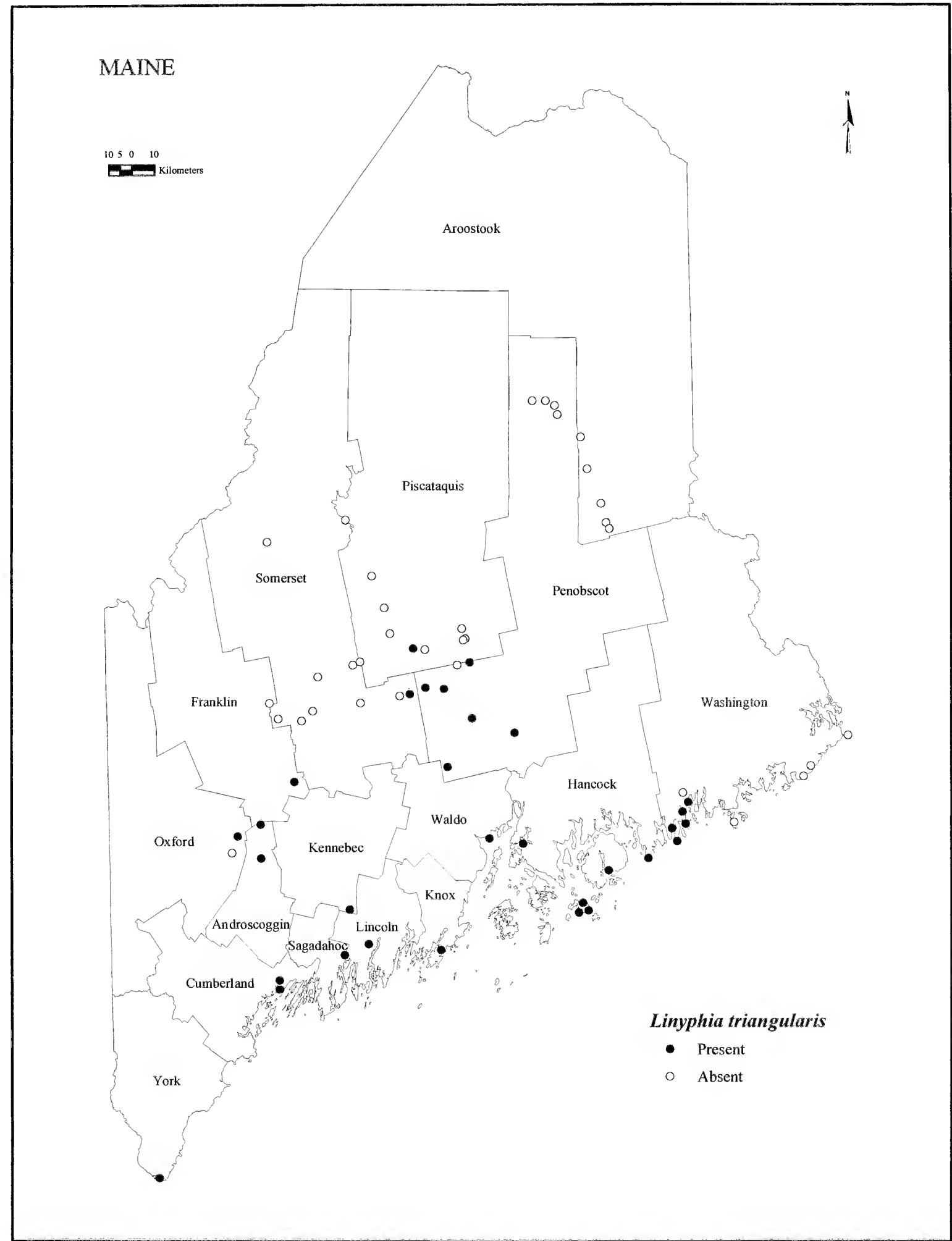
Survey results.—During August–September, 1999, 15–20 minute searches were made at numerous localities and among diverse habitats in rural Maine. The survey yielded 64 specimens of *L. triangularis* from the counties

of Androscoggin, Franklin, Kennebec, Knox, Lincoln, Oxford, Penobscot, Piscataquis, Sagadahoc, Somerset, and Waldo (Map 1); none were found in Aroostook County. Additional searches during August–September, 2000, failed to yield specimens of this exotic spider in mid, northern, and far “downeast” Maine (Map 1). Of Maine’s 16 counties, only Aroostook County remains to yield specimens of *L. triangularis*. The chronological and geographic distributions of our records suggest that the species might be moving inland from a coastal locus or loci. Thus far, *L. triangularis* has not been found in Quebec (Paquin et al. 2001) or in New Brunswick (Buckle et al. 2001).

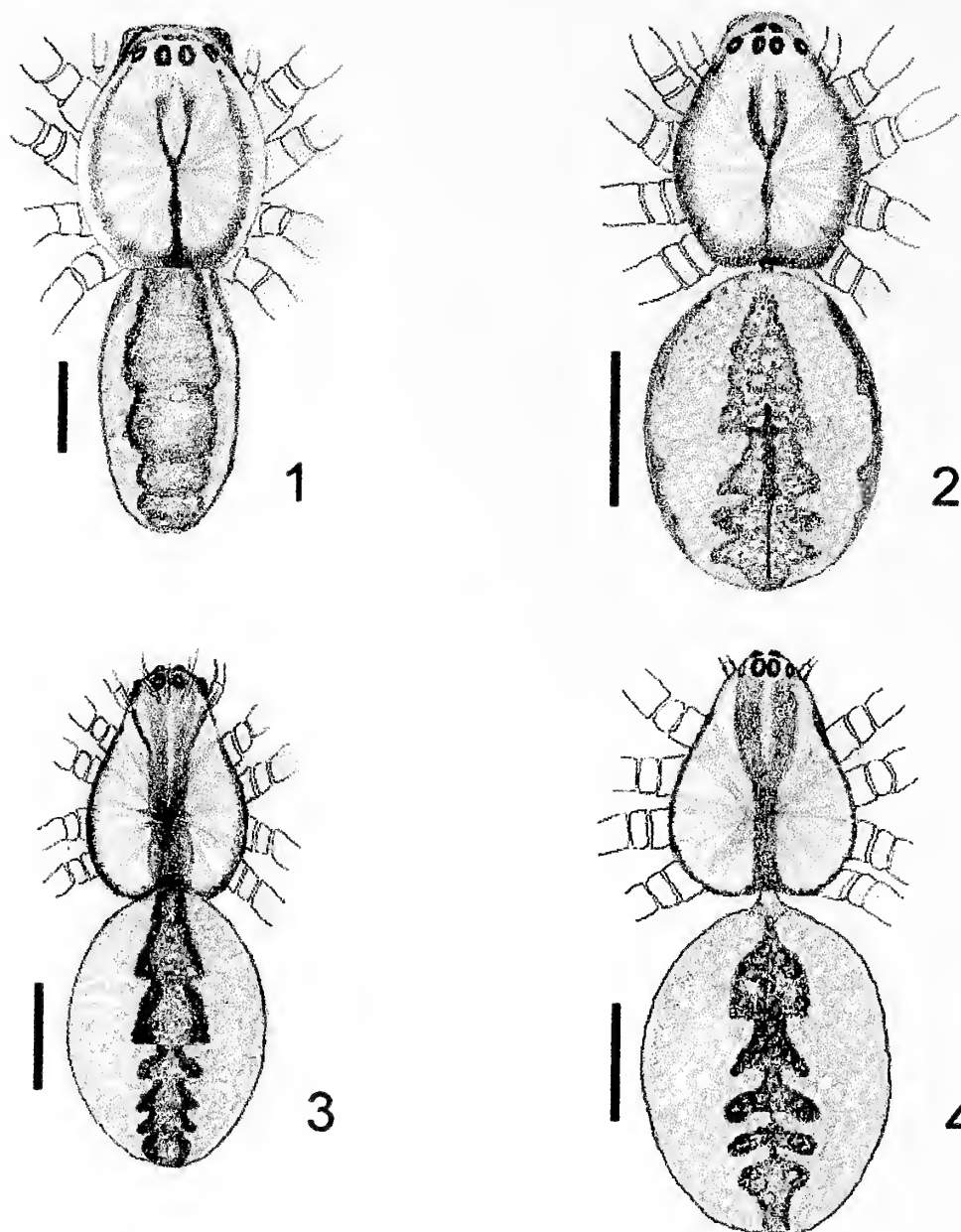
Introductory date, origin, & mode.—The actual date of arrival, source or origin of emigration, and mode of travel are unknown. Historical collections of spiders in New England provide some evidence that *Linyphia triangularis* arrived recently (i.e., within the last half-century) in Maine. In the late 1800’s and early 1900’s, James H. Emerton and Elizabeth B. Bryant collected spiders in Maine and other New England states, but none of their published lists (see Bonnet 1945) include *L. triangularis*. During the last half-century, spiders have been collected extensively in New England and the Maritime Provinces; e.g., Charles D. Dondale, James H. Redner, and associates in Ontario, Quebec, New Brunswick, and Newfoundland; Robert L. Edwards in Cape Cod, Massachusetts; Benjamin J. Kaston in Connecticut; and Herbert W. Levi in Massachusetts, New Hampshire, Maine and other New England states. None of these collections yielded specimens of *L. triangularis*.

Prior to the discoveries in Maine, the known geographic distribution of *L. triangularis* included the Palearctic region from southern, western, and northern Europe to Siberia and China in the east (Helsdingen 1969). The species is very common in the British Isles (Locket & Millidge 1953) and in Scandinavia (Nielsen & Toft 1990). With the recent expansion of worldwide commerce, any one or more countries in the Palearctic region could serve as the origin(s) of emigration of *L. triangularis* to North America.

Description, webs, and life history.—Descriptions and illustrations of *Linyphia triangularis* are provided by Helsdingen (1969) and Roberts (1993, 1995), and include illustrations of the male and female genitalia. The



Map 1.—Distribution of collection and survey sites in Maine for the Palearctic sheet-line weaver, *Linyphia triangularis* (Clerck, 1757). Closed circles, *L. triangularis* present, all data inclusive (1983–2000); open circles, *L. triangularis* not present in 1999 or 2000.



Figures 1–4.—Dorsum of carapace and abdomen. 1, 2. *Linyphia triangularis* collected in Maine. 1. Male; 2. Female; 3, 4. *Pityohyphantes* sp. collected in Maine. 3. Male; 4. Female. Scale bars = 1 mm. (Drawings by N. Sferra).

color pattern of *L. triangularis* closely resembles that of the North American *Pityohyphantes costatus* (Hentz 1850); dorsally, both species have a bifurcated, “tuning-fork” marking on the carapace, and a herring bone pattern on the abdomen (Figs. 1–4). The latter is less evident in *L. triangularis* males (Fig. 1). The markings of *L. triangularis* also resemble those of *P. phrygianus* (C. L. Koch 1836), another European immigrant in Maine, but less common than *P. costatus*. Ventrally, the femora of *L. triangularis* are devoid of dark spots, while black or dark-brown spots are usually present on the femora of *P. costatus* and *P. phrygianus* (cf. Roberts 1993, Part 2, plates 231 & 233). Unlike *Pityohyphantes*, the tuning-fork markings do not extend to the posterior eye rows in *L. triangularis* (Figs. 1–2).

The web of *L. triangularis* has been described and illustrated by Nielsen (1931),

Bristowe (1958), Jones (1983), and Preston-Mafham (1984). It consists chiefly of a flattened sheet, slightly arched in the center, and held in place by scaffolding threads above and below the sheet. The web lacks a retreat, with the resident spider hanging upside-down near the center of the sheet. The webs of *L. triangularis* in Maine more closely resemble the webs of *Pityohyphantes* species than those of *Neriene radiata* (cf. Roberts 1995, p. 74).

The species is univoltine in Europe, overwintering as eggs in leaf-litter beneath trees and shrubs (Turnbull 1960). Juvenile spiderlings emerge from the egg sac in the spring (May), and reach maturity by late July or August (Toft 1978, 1989). Development is pro-tandrous, with males reaching adulthood about a week earlier than females. The sexually mature males enter the webs of subadult females, where they remain until the female

reaches maturity (Toft 1989; Nielsen & Toft 1990). Shortly afterwards, mating takes place in the web (Herberstein 1997; Stumpf 1990), followed by oviposition in October or November (Nielsen & Toft 1990). The life history of *L. triangularis* in North America remains to be studied.

Potential impacts.—What are the potential impacts of *L. triangularis* on the native spider and insect faunas in Maine? Such impacts could be beneficial, neutral, or detrimental. In northern Europe, *L. triangularis* usurps the webs of conspecifics and congenics (Toft 1987, 1990). Though native *Linyphia* species are absent in eastern North America (Helsdingen 1969; Buckle et al. 2001), *L. triangularis* could invade the webs of associated species such as *Frontinella communis*, *Pityohyphantes costatus*, or *Nerienne radiata*. If so, will this alien spider compete with native species for microhabitat space and food, or are such resources sufficiently abundant to provide niche partitioning and species coexistence? Perhaps differences in developmental phenologies or other ecological-behavioral parameters will minimize impacts between invader and native species.

We suspect that biodiversity will be affected by this introduction. Collectively, invasion by exotics is the second most prevalent cause of species endangerment after habitat loss (Wilson 1992; Czech et al. 2000). For example, in some regions of northeastern North America, the native *Steatoda borealis* (Hentz 1850) has been displaced by the European *S. bipunctata* (Linnaeus 1758) (Nyffeler et al. 1986). Will native sheet-line weavers and other spiders be displaced by *L. triangularis*? These and other questions pose unique challenges to researchers and resource managers alike. See Cox (1999 & lit. cited) for a review of potential impacts of invasive exotics.

Linyphia triangularis meets 7 of the 8 criteria that characterize a successful invader (Ehrlich 1986), i.e., 1) abundant in original range; 2) polyphagous instead of monophagous or oligophagous; 3) short generation time; 4) fertilized female able to colonize alone; 5) larger than most relatives; 6) associated with *Homo sapiens*; and 7) able to function in a wide range of physical conditions. Only its genetic variability, compared to that of non-invaders, remains to be ascertained. Because this alien species is free from

its natural enemies of origin, populations in Maine are apt to expand rapidly unless tempered by native parasites, predators, and pathogens.

We conclude that *L. triangularis* has successfully invaded and established breeding populations in Maine. The future of these populations and their potential impacts on Maine's diverse insect and spider faunas warrant further investigation.

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INFLUENCE OF FEEDING REGIME ON BODY SIZE, BODY CONDITION AND A MALE SECONDARY SEXUAL CHARACTER IN *SCHIZOCOSA OCREATA* WOLF SPIDERS (ARANEAE, LYCOSIDAE): CONDITION-DEPENDENCE IN A VISUAL SIGNALING TRAIT

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ABSTRACT. Male *Schizocosa ocreata* (Hentz) wolf spiders (Araneae, Lycosidae) have tufts of elongated, dark bristles on the patella and tibia of the forelegs, which are involved in visual signaling. Previous research has suggested that these tufts are used by females as a criterion in mate choice, raising the question of whether they might serve as indicators of male condition. We tested the hypothesis that tufts are condition-dependent indicator traits with a laboratory rearing study subjecting spiders to lifelong feeding regimens representing successful (high food) and unsuccessful (low food) foraging history, after which males were measured upon reaching adulthood. Mortality varied significantly with experimental treatment, and had a disproportionate impact on some egg sacs assigned to the low food treatment. Age at sexual maturity and several body size measures varied significantly with feeding history. Well-fed spiders survived better, matured earlier, were significantly larger, and were in relatively better condition (measured as a residual body condition index) than deprived spiders. Additionally, well-fed spiders had significantly larger relative tuft size (scaled for body size). These data suggest that male body size, condition and a conspicuous male signaling trait vary with feeding history, and thus have the potential to serve as “honest indicators” of male quality in mate choice.

Keywords: Feeding, condition-dependence, male secondary sex characters, wolf spiders, Lycosidae, *Schizocosa*

Signals used by males during courtship and mating have been studied extensively, and there is general agreement that they function in species recognition (Colgan 1983; Alcock 1998) and also in female mate choice (Andersson 1994; Alcock 1998). There is growing evidence that signals such as elaborate male morphological characters and complex display behaviors convey information to females about male condition or quality, and that females choose mates based on these traits (e.g., “handicap” or “good genes” models; Zahavi 1975; Clutton-Brock & Albon 1979; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984; Zuk 1991; Houde & Torio 1992; Andersson 1994; Kotiaho et al. 1998). Because these elaborate male traits and displays are often

costly to produce, and vary in size or expression with the condition of the male, they are deemed “honest” indicators of male quality; only males in the best condition are able to express larger traits (Andersson 1986; Grafen 1990; Johnstone 1995). Additionally, male decorations may serve as “amplifiers” i.e., traits that draw attention to or enhance discrimination of other condition-indicating signaling traits (Hasson 1991; Hebets & Uetz 2000; Taylor et al. 2000).

Several spider families with well-developed visual capabilities (e.g., Salticidae, Lycosidae) utilize visual signaling in courtship communication (Jackson 1982; Richman 1982; Stratton 1985; Uetz 2000). Adult males of these families often exhibit conspicuous visual signaling traits, widely assumed to function in species recognition, driven by selection from potential cannibalism by females (Crane 1949; Jackson 1982; Richman 1982; Uetz & Stratton

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1983; Stratton 1985; Elgar 1991, 1992; Newman & Elgar 1991; Hebets & Uetz 2000; Uetz 2000). Even so, the role of sexual selection via female mate choice has also been considered as a potential force in the evolution of male morphology and decorations (Peckham & Peckham 1889; Jackson 1981; Clark & Uetz 1993; Scheffer et al. 1996; McClintock & Uetz 1996; Elgar 1998; Uetz 2000).

While the question of whether male traits convey information useful to females in evaluating mate quality is central to understanding sexual selection (and the subject of much research with other animal taxa), it is not well understood for spiders. In one extensively-studied species, the wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865), females choose mates based on the percussive "drumming" display of males (Kronstedt 1996; Parri et al. 1997). These displays are energetically expensive and condition-dependent, thereby serving as honest indicators of male quality (Mappes et al., 1996; Kotiaho et al. 1998; Kotiaho 2000). In this study, we examine the influence of feeding history and body condition on a male secondary sexual character (leg tufts) used in visual signaling by the brush-legged wolf spider, *Schizocosa ocreata* (Hentz 1844).

Among the most common spiders in Eastern North America, *S. ocreata* is a well-studied model species whose visual and vibratory signaling behaviors have been demonstrated to serve in species recognition and reproductive isolation (Stratton & Uetz 1981, 1983, 1986; Uetz 2000), as well as mate choice (Scheffer et al. 1996; McClintock & Uetz 1996; Hebets & Uetz 1999, 2000; Uetz 2000) and male-male aggression (Aspey 1977a, b). These spiders exhibit sexual dimorphism i.e., adult male *S. ocreata* have conspicuous tufts of bristles on the forelegs (used in visual courtship displays) that are absent in females and juveniles. While some previous studies suggest that variation in this conspicuous male visual signaling trait is related to male condition and might influence mate choice (see review in Uetz 2000), the basis of variation in male tufts is currently unknown. In this study, we test the hypothesis that the size of these tufts is condition-dependent, and reflects foraging success, with laboratory rearing studies and measurement of subsequent spiders.

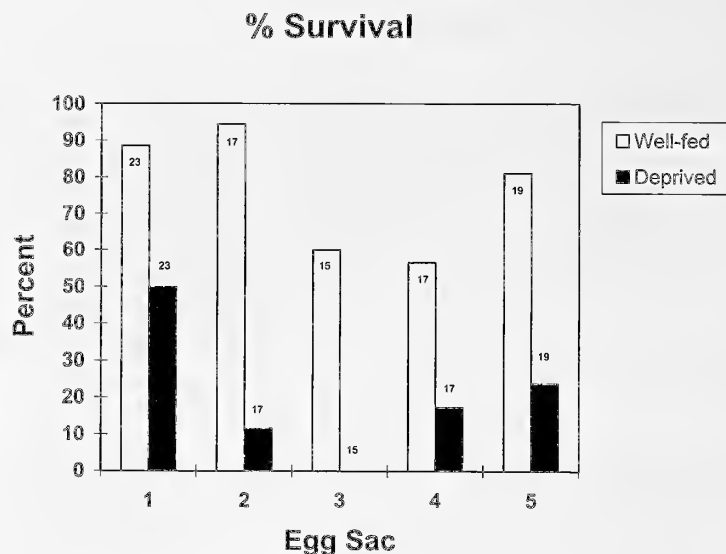


Figure 1.—Percent of *S. ocreata* raised under different feeding regimes (numbers above bars indicate initial N) surviving to adulthood from each of five egg sacs (open bars = well-fed; dark bars = deprived).

METHODS

Wolf spiders used in this study were raised from egg sacs produced by females that were collected from the field as immatures and mated in the lab. Spiders (parents) were collected as penultimate instar juveniles in May and June 1995 from deciduous forest habitat at the Cincinnati Nature Center Rowe Woods facility in Clermont County, Ohio. Representative specimens of this population are located in a number of museum collections, including the Cincinnati Museum of Natural History, the Ohio State University collection, the Museum of Comparative Zoology and the US National Museum of the Smithsonian Institution.

Spiders (parents) were maintained in the lab until maturity under identical controlled conditions at room temperature (23–25 °C) in an environment with stable humidity and a 13:11 L:D photoregimen. Spiders were individually housed in opaque containers (12 cm diam., 5 cm ht.), with clear lids (so spiders are exposed to light cues but are visually isolated from each other). Spiders were provided water ad libitum from a soaked cotton dental wick, and fed 2–3 live domestic crickets (*Acheta domestica* L.) twice weekly.

Female wolf spiders with egg sacs ($n = 5$) were selected at random from a pool of individuals previously mated in the laboratory (each female was paired with a male at random and allowed to mate). Because just-hatched wolf spiders spend a short period of time riding on the mother's abdomen before

dispersing (ca. one week), we waited until spiderlings (offspring of above-mentioned matings) were dispersing to isolate them, then assigned approximately half of the spiderlings from each egg sac at random to the two feeding regime treatments. Numbers of spiderlings used varied from 30–46 per egg sac, with a total of approximately 90 spiders/experimental treatment. Spiders were then maintained in the laboratory until maturity under the controlled environmental conditions described above. Each spider was given a unique identification number, and spiders were weighed and fed appropriately sized springtails (*Collembola*) and/or domestic crickets (*Acheta domestica* L.) on a weekly basis. Two feeding regimes were maintained as a 4:1 ratio diet difference based on previous studies (Jakob et al. 1996): 1. well-fed, an amount equal to each spider's body mass twice per week; and 2. deprived, an amount equal to half of each spider's body mass once per week.

Measurements and statistical analyses.—Each male spider was measured at maturity from a digitized image (produced with a JVC GN-8 videocamera with a macro lens, mounted at a fixed distance above the specimen on a 1 mm grid background). Digital measurements were made using NIH Image, a digital measurement program. We measured two frequently used body size measures: body length (BL) and cephalothorax width (CW). Spiders were rotated and placed on their right side to provide a lateral view of legs I, which was used to measure tuft area (TA) as a scribed polygon (area in mm) in NIH Image. Each tuft was measured three times, and a two-way ANOVA was used to determine measurement repeatability (Swaddle et al. 1994). As certain aspects of spider size are more or less fixed at adulthood (e.g., cephalothorax width) while others vary with feeding and water intake (e.g., weight, body length), we also calculated indices of body condition (as in Jakob et al. 1996; Kotiaho 1999; Marshall et al. 1999).

Data were tested for normality and transformed with natural log (ln) or other transformations where appropriate. Data were subjected to statistical analyses using a model with feeding treatment (high food/low food) nested within egg sac. Survival data were analyzed with logistic (log-likelihood) regression analysis, while all other data were analyzed with nested ANOVA. Subsequent

comparisons between treatments were made using Tukey post-hoc tests or t-tests, with adjustments for equal or unequal variances. All analyses were conducted using the software package JMP ver. 4.0 (SAS Institute).

RESULTS

Survival to adulthood varied significantly with both treatment and egg sac (Whole model: $df = 9$, $X^2 = 87.397$, $P < 0.0001$; Treatment effects–egg sac: $df = 4$; $X^2 = 18.995$, $P = 0.0008$) and feeding treatment (nested within egg sac); $df = 5$; $X^2 = 74.567$; $P < 0.0001$). Approximately 76% of spiders in the well-fed treatment survived to adulthood, but only 20.5% of the deprived treatment survived (Fig. 1).

Age of male spiders at adulthood varied significantly between treatments (analyzed as nested within egg sacs; $F_{3,4} = 14.85$; $P < 0.001$), but not egg sac ($F_{4,4} = 1.61$; $P = 0.195$). Males from the well-fed treatment matured significantly earlier than those from the deprived treatment across all egg sacs (Fig. 2). For age of females at adulthood, there was also a significant treatment effect (analyzed nested within egg sac; $F_{3,4} = 3.07$; $P < 0.035$), but no effect of egg sac ($F_{4,4} = 0.964$; $P = 0.434$). Females from the well-fed treatment matured significantly earlier than those from the deprived treatment across all egg sacs (Fig. 3). Overall, males matured approximately 10 days prior to females, which is often typical of *S. ocreata* in the field during the Spring breeding season.

Age at Sexual Maturity - Males

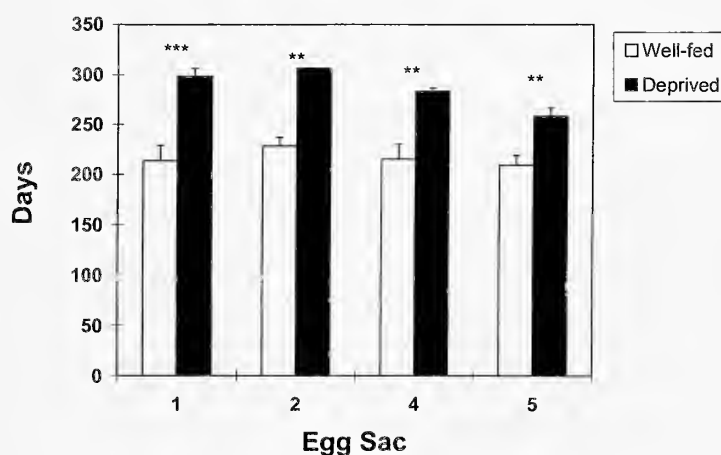


Figure 2.—Mean time to maturity (days to adulthood) for male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

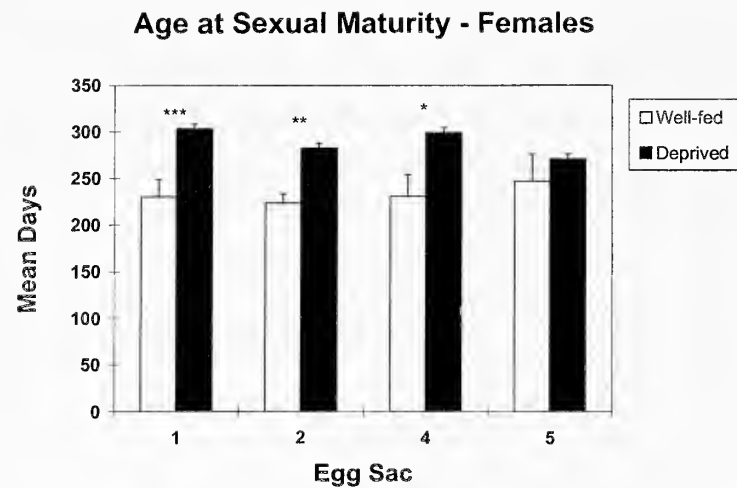


Figure 3.—Mean time to maturity (days to adulthood) for female *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

As one egg sac had no survivors in the deprived treatment, it was dropped from subsequent analysis of adult male measures. Morphological parameters related to overall size (BL, CW) and body condition (residual index) measured for adult males varied significantly with level of feeding, as well as with egg sac in the case of body length (Table 1, Figs. 4–6). Well-fed spiders were significantly larger in size than deprived spiders in most cases, as reflected in data for body length and cephalothorax width (Figs. 4, 5). Body condition varied significantly with treatment, but not egg sac (Table 1); overall, well-fed spiders exhibited higher body condition indices (Fig. 6). Given the low sample sizes for some of the

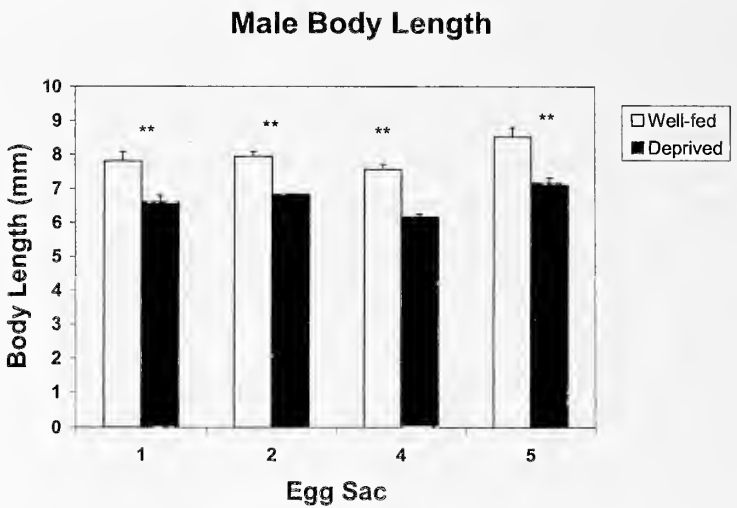


Figure 4.—Body length (mm) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

egg sacs, these data must be interpreted with caution.

Repeatability of measurements of tuft area (mm) was determined with two-way ANOVA, as recommended by Swaddle et al. (1994). Between-individual variance was greater than within-individual variance for tuft area ($F_{1,2} = 210.5$, $P < 0.001$), indicating low measurement error (and high repeatability). However, subsequent analyses of tuft area (overall means of three measures for each leg tuft) revealed a consistent measurement bias owing to specimen placement and perspective. To avoid error arising from this bias, we used only the measurement of the (larger) left leg in subsequent analyses. To examine for the influence of overall body size, condition, egg

Table 1.—Nested Analysis of Variance for size male and body condition.

Source	df	MS	F	P
Body length (mm)				
Egg sac	3	1.423	4.266	0.012
Treatment (egg sac)	4	3.545	10.62	<0.0001
Error	33	0.333		
Cephalothorax width (mm)				
Egg sac	3	0.253	2.142	0.114
Treatment (egg sac)	4	0.820	6.929	0.0004
Error	33	0.118		
Body Condition Index*				
Egg sac	3	0.042	0.657	0.584
Treatment (egg sac)	4	0.206	3.185	0.026
Error	33	0.065		

* (residual of \ln Cube Root Abdomen Volume $\times \ln$ CW)

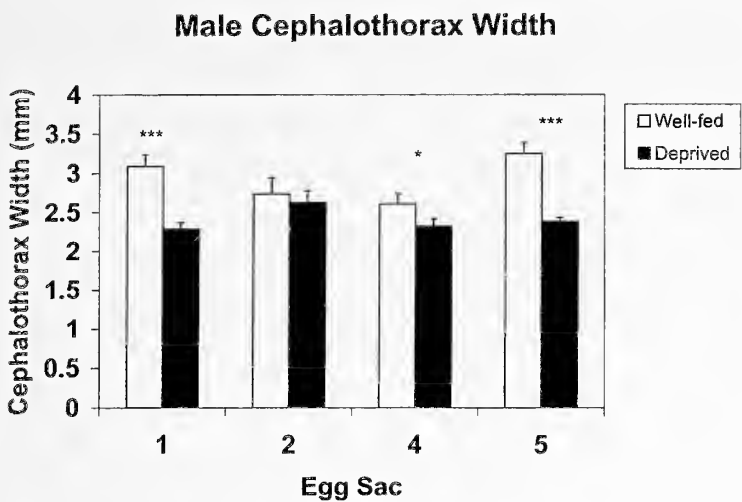


Figure 5.—Cephalothorax width (mm) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

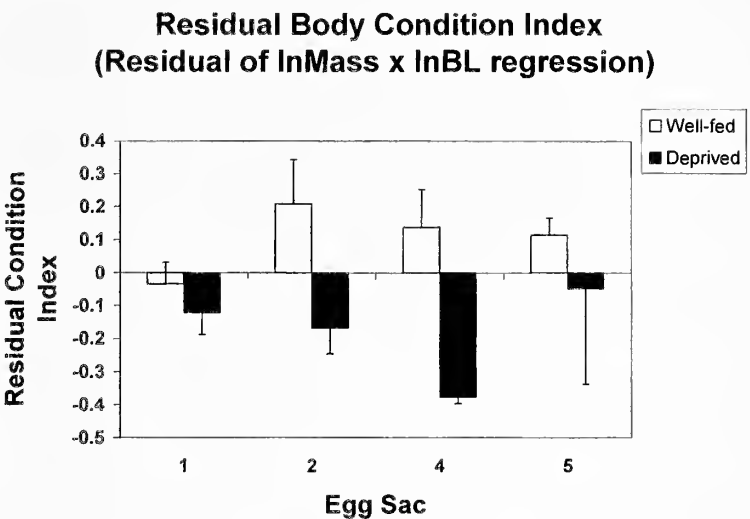


Figure 6.—Body condition index (residual of ln cube root abdomen volume vs. ln CW) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

sac and treatment on tuft area, mean left tuft area was subjected to a stepwise elimination multiple regression analysis with those parameters as independent variables (Table 2). This multiple regression was significant ($F_{5,40} = 47.734$, $P < 0.001$, $R^2 = 0.715$), but only two variables (treatment and leg length) had significant effects ($P < 0.001$). However, given the potential colinearity of tuft size and leg I length, we tested the hypothesis that feeding regime influences tuft size with an additional analysis. As ANOVA of leg I length revealed a significant effect of CW ($F_{1,37} = 25.303$; $P < 0.0001$), but no treatment effect ($F_{1,37} = 0.0076$; $P = 0.931$) nor interaction of CW x treatment effect ($F_{1,37} = 3.45$; $P = 0.071$), we felt justified in using a scaled tuft size index (the residual of the regression of tuft area x leg I length). A nested ANOVA of residual tuft area revealed a significant effect of treatment ($F_{4,33} = 3.533$; $P = 0.016$), but not egg sac ($F_{3,33} = 1.39$; $P = 0.262$). Regression of

leg tuft area x leg length revealed nearly identical slopes, but significantly different intercepts between experimental feeding treatments ($F_{1,1} = 23.47$, $P < 0.0001$, $R^2 = 0.713$). Tufts were significantly larger across the range of leg length variation for males in the well-fed treatment (Fig. 7).

DISCUSSION

At first, the results of this study might not seem suprising, as a number of other studies have shown that spiders subjected to variation in feeding regime survive differently, mature at different rates and vary in size and activity at adulthood (Anderson 1974; Riechert & Harp 1987; Uetz et al. 1992; Toft & Wise 1999; Walker et. al. 2000). Additionally, as male morphological characters often covary with body size, it might also be expected that they would vary as a consequence of different feeding regimes. However, even with the in-

Table 2.—Stepwise multiple regression analysis of tuft size for male *Schizocosa ocreata* reared under separate food regimes vs. factors of potential influence. Factors are listed in order of stepwise elimination.

Parameter	B (slope)	t	P
Body length (mm)	0.136	0.240	0.816
Cephalothorax width (mm)	−0.220	−0.280	0.782
Body Condition Index*	−0.564	−0.420	0.676
Egg sac	−0.201	−1.360	0.481
Treatment	−0.201	−4.70	<0.0001
Leg I length	0.316	4.309	<0.0001
Final Model (Treatment, Leg I length): $R^2 = 0.715$; $F_{5,40} = 47.734$; $P < 0.0001$			

* (residual of ln Cube Root Abdomen Volume × ln CW)

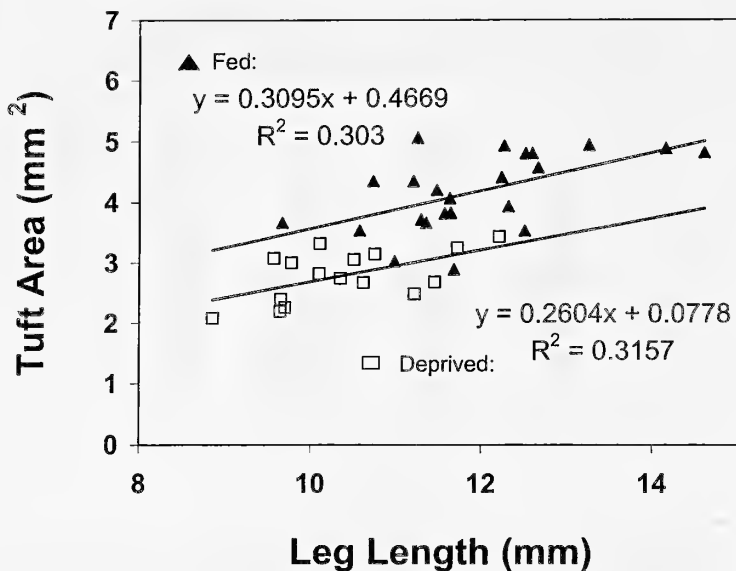


Figure 7.—Linear regression of foreleg tuft size (left tuft area in mm²) vs. leg I length (mm) for adult male *S. ocreata* raised under different feeding regimes: well-fed (filled triangles) and deprived (open squares).

fluence of body size held constant, the leg tufts of male *S. ocreata* vary significantly with lifelong feeding regime, which demonstrates the potential for this male character to serve as an “honest” indicator of condition based on previous foraging success. Given that previous research has implicated these tufts in female mate choice, findings of this study may have broader implications.

Like a number of other wolf spiders, male *S. ocreata* have elongated, dark bristles on the patella and tibia of the forelegs, creating “tufts” that may function as signals indicating condition, or as signal amplifiers (Uetz 2000; Hebets & Uetz 2000). Several species in the genus *Schizocosa* and the family Lycosidae possess similar decorations (Miller et al. 1998; Hebets & Uetz 2000), and a recent phylogenetic analysis suggests that male tufts are a derived character that has evolved independently several times in this genus (G.E. Stratton, pers. comm.). Scheffer et al. (1996) found that female *S. ocreata* receptivity varied with the presence or absence of these male tufts (manipulated by shaving live males), but only when vibratory cues were absent. They suggested that tufts might increase the efficacy of visual signaling in complex litter habitats, which can constrain vibration transmission. Several other studies with live males as well as manipulated video stimuli indicate that female receptivity to visual courtship signals from males may vary with the size and symmetry of tufts (Uetz 2000). Female receptivity

is lower when tufts are absent (McClintock & Uetz 1996; Hebets & Uetz 2000), asymmetric (Uetz et al. 1996; Uetz & Smith 1999), or small in size (McClintock & Uetz 1996; Uetz 2000).

If costly ornaments or displays reflect some heritable characteristic of the male related to viability, both the display and female preference for males based on such display traits would be favored by selection (Andersson 1996). Male traits may reflect quality over different time scales, as “static” morphological traits that are fixed at adulthood may reflect long-term influences (e.g., lifetime foraging success), while body condition indices and “dynamic” behavioral display traits may indicate short-term changes in condition (e.g., energy reserves) (see Gerhardt 1991; Nicoletto 1991, 1993; Moller & Pomiankowski 1993; Hill et al. 1999; Parten & Marler 1999). In the best-studied case of male signaling and female mate choice in spiders, females of the wolf spider *H. rubrofasciata* prefer males with higher drumming rates (Parri et al. 1997). Drumming rates vary with size and condition of males, at least in the short term, and the high cost of this energetically expensive display has a negative impact on male survival during the breeding season (Mappes et al. 1996; Kotiaho et al. 1998; Kotiaho 2000). Results of our study suggest that leg tufts in *S. ocreata* are a static trait that reflects variation in male condition arising from long-term feeding influences. However, even though tuft size in *S. ocreata* is fixed at adulthood, wearing from various sources may damage tufts and diminish their size over the breeding season (P.W. Taylor & G. Uetz, pers. obs.).

The adaptive significance of decorative leg tufts in male courtship behavior and female mate choice, as well as the evolution of these traits, is not fully understood in the genus *Schizocosa*. There is currently no evidence that suggests females of this species gain any direct or indirect benefits by choosing or discriminating among males on the basis of tuft size (or for that matter any other male trait). Ultimately, it may be that these traits serve multiple roles: as species-specific mate recognition cues, as a means of gaining female attention in a complex visual/vibratory environment, as indicator traits or as amplifiers of condition-indicating behaviors. This study demonstrates that in addition to a number of

functions previously suggested for these traits, the potential also exists for male leg tufts to serve as visual signals indicating male condition and previous foraging success.

ACKNOWLEDGMENTS

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THE FIRST OLD WORLD SPECIES OF PHRYNIDAE (AMBLYPYGI): *PHRYNUS EXSUL* FROM INDONESIA

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ABSTRACT. A new species of *Phrynus*, *P. exsul*, from the Indonesian island of Flores, represents the first member of the family found outside of the New World.

Keywords: Whip-spiders, Phrynidae, Indonesia, Flores, new species

The whip-spiders (Amblypygi) of Asia and the Australasian region are currently represented by five genera in three families. The Charinidae includes species of *Charinus* Simon 1892 (a senior synonym of *Charinides* Gravely 1911, see Weygoldt (2000)), several species of *Sarax* Simon 1892 (a senior synonym of *Phrynichosarax* Gravely 1915, see Weygoldt (2000)), and a single species of *Catageus* Thorell 1889. The Charontidae are endemic to the Australasian region with two genera, *Charon* Karsch 1879 and *Stygophrynus* Kraepelin 1895. The Phrynichidae includes several species of *Phrynichus* Karsch 1879 that were recently revised by Weygoldt (1998). Therefore, it was surprising to find an adult male whip-spider collected from a cave situated on the Indonesian island of Flores that possesses all the major diagnostic features of the Phrynidae. Many different genera were attributed to the family (or its synonyms) during the 19th century, but the Phrynidae are presently regarded to be confined to an area ranging from southern U.S.A. to South America (Weygoldt 2000), where four Recent genera and a single genus from Tertiary amber deposits are represented in two subfamilies. The Heterophryninae consist of numerous species of *Heterophrynus* Pocock 1894, found only in northern South America. The Phryninae consist of a single species of *Acanthophrynus* Kraepelin 1899 from Mexico and south-western U.S.A., 17 species of *Paraphrynus* Moreno 1940, and 21 Recent species of *Phrynus* Lamarck 1801 (e.g., Mullinex 1975; Quintero 1981). The status and affinities of the Late Oligocene-Early Miocene *Electrophrynus mirus* Petrunkevitch 1971 from Chiapas amber are unknown.

The identity of the species was kindly confirmed by Dr. Peter Weygoldt who later pro-

vided a second male from the same cave. Although it is generally not desirable to name new taxa based upon so few specimens, it appears that further material from Flores will not be forthcoming in the near future, and a description of this remarkable species is presented here.

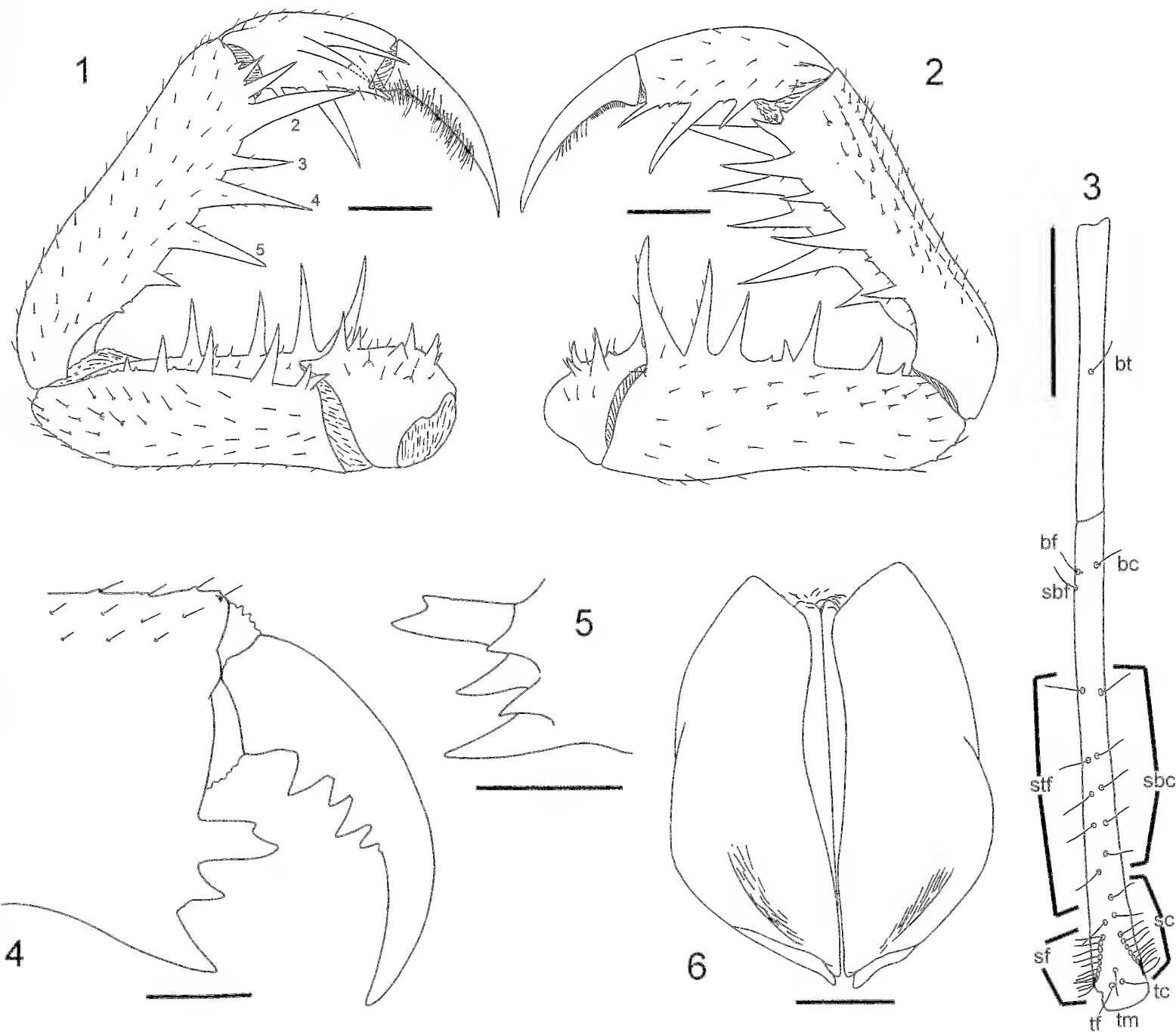
METHODS

The specimens are lodged in the Western Australian Museum, Perth (WAM) and the Muséum d'histoire Naturelle, Genève (MHNG). Terminology largely follows Weygoldt (1996, 2000), with the exception of the nomenclature of the pedipalp and leg segments, which follows Snodgrass (1948), Harvey & West (1998) and Shultz (1999). Therefore, the pedipalp consists of six segments: coxa, trochanter, femur, patella, tibia and tarsus, plus a terminal apotele (or claw). The legs consist of seven segments: coxa, trochanter, femur, patella, tibia, metatarsus and tarsus, plus the apotele (or claws). This terminology allows for the segments to be homologised with that used for other arachnids. The terminology used for the spination of the pedipalps follows Weygoldt (2000), rather than Quintero (1981). The distance of each pedal trichobothrium from the basal margin of the leg segment is expressed as a percentage of the total length of the segment and presented in parentheses.

SYSTEMATICS

Family Phrynidae Blanchard 1852
Subfamily Phryninae Blanchard 1852
Genus *Phrynus* Lamarck 1801

Tarantula Fabricius 1793: 432. Type species: *Phalangium reniforme* Linnaeus 1758, by subsequent designation of Karsch 1879.



Figures 1–6.—*Phrynus exsul* new species, male holotype 1. Left pedipalp, dorsal; 2. Left pedipalp, ventral; 3. Tibia IV segments 3 and 4, lateral; 4. Left chelicera, internal, most pilosity omitted; 5. Left chelicera, detail of teeth, external; 6. Genitalia, dorsal. Scale lines = 2 mm (Figs. 1–3), 1 mm (Figs. 4–6).

Phrynus Lamarck 1801: 175. Type species: *Phalangium palmatum* Herbst, in Lichtenstein & Herbst 1797, by subsequent designation of Karsch 1879.

Admetus C.L. Koch 1850: 81. Type species: *Phalangium palmatum* Herbst, in Lichtenstein & Herbst 1797, by subsequent designation of Simon 1892.

Neophrynus Kraepelin 1895: 23–24. Type species: *Phalangium palmatum* Herbst, in Lichtenstein & Herbst 1797, by original designation.

Diagnosis.—Species of *Phrynus* differ from those of *Paraphrynus* by the relative length of the dorsal spines on the pedipalpal patella (Mullinex 1975; Quintero 1981): in *Phrynus* dorsal spine 3 is shorter than spines 2 and 4, whereas in *Paraphrynus* dorsal spines 3 and 4 are shorter than spines 2 and 5.

Remarks.—An unresolved problem in the taxonomy of the Phrynidae is the status of the genera *Tarantula* Fabricius 1793 and *Phrynus*. Quintero (1981, 1982) discussed the problem in detail, and opted to retain the name *Phrynus* over *Tarantula*, despite the priority of the latter name. The International Commission on Zoological Nomenclature has yet to make a decision on the application, and I therefore maintain the prevailing usage of *Phrynus*.

Phrynus exsul new species
Figs. 1–6

Material examined.—Holotype male from Gua Cermin, near Labuan Bajo, Flores, Indonesia, 8°33'S, 119°55'E, 25 May 1990, R.E. Johnstone, R.A. How (WAM 98/1591). Para-

type: 1 male, same locality, 22 January 2001, C. Deeleman (MHNG).

Etymology.—The specific epithet refers to this species being the sole phrynid that is currently known from the Old World (*exsul*, Latin, a banished person, in exile).

Diagnosis.—*Phrynus exsul* differs from all other members of the family by the increased number of trichobothria on the distitibia, for example on distitibia IV, where rows sbc and stf are each composed of 5 trichobothria (Fig. 3).

Description.—Male: Carapace, pedipalps and legs reddish-brown; tergites slightly paler; femora of legs with barely discernible broad annulations. All setae acicular. Carapace: anterior margin slightly concave, with numerous setiferous tubercles; median and lateral eyes not reduced in size; carapace with numerous fine setiferous tubercles as well as many small non-setiferous tubercles; frontal process concealed. Sternum tripartite, each sternite not expanded; anterior sternite with two very stout distal setae and numerous smaller setae, mostly clustered in basal third; median sternite with 3–5 small setae; posterior sternite 3–7 small setae. Chelicera (Figs. 4, 5): hand with 3 teeth on external margin, the two dorsal teeth on a common base (Fig. 5); 3 teeth on internal margin, the most dorsal tooth bicusped with lower tooth the largest (Fig. 4); movable finger with 4 large teeth and 1 very small distal tooth along inner margin (Fig. 4). Pedipalps (Figs. 1, 2) stout; trochanter with several spines on antero-dorsal margin; femur with 6 major spines and several minor spines on antero-dorsal margin, spine 4 largest, antero-ventral margin with 6 major spines and several minor spines, spine 6 the longest; patella with 6 major spines on antero-dorsal margin, spine 3 smaller than spines 2 and 4, antero-ventral margin with 5 major spines, spines 2 and 4 the longest, all spines without basal sub-spine; tibia with 3 spines on antero-dorsal margin, spine 1 with 3 small denticles in basal half, dorsal margin with 4 small denticles; antero-ventral margin with 3 major spines, spine 2 largest, with 1 small denticle between spine 2 and 3, and 3 small denticles between spines 1 and 2; tarsus with single minute spine situated dorsal to cleaning organ; apotele completely fused to tarsus, without suture line or division; cleaning organ composed of a ventral row of large setae and a dorsal

row of small setae. Legs: leg I with 34 (holotype), 31 (paratype) tibial, 44 (holotype) 45 (paratype) metatarsal and 23 (holotype), 21 (paratype) tarsal segments; 12th last segment of tarsus I with plate organ; femur I 2.41 (3.54) times longer than carapace; tibiae II and III with 2 segments, tibia IV with 4 segments, third segment with 1 trichobothrium, bt (0.51), fourth segment (distitibia) with 36 trichobothria (Fig. 3): bf (0.12), bc (0.11), sbf (0.15), stf₁ (0.35), stf₂ (0.49), stf₃ (0.56), stf₄ (0.62), stf₅ (0.72), sbc₁ (0.36), sbc₂ (0.49), sbc₃ (0.55), sbc₄ (0.62), sbc₅ (0.68); distitibiae II and III with similar, increased, numbers of stf and sbc; tarsi II, III and IV each with 4 segments; last segment with oblique slit; pulvilli absent. Genitalia as in Fig. 6.

Dimensions (mm), holotype (paratype): Body length (without chelicerae) 27.5 (38.0). Carapace: median length 8.95 (13.35), width 13.77 (19.83). Pedipalps: trochanter length 4.10 (6.22), width 2.53 (4.03); femur length 7.52 (14.39), width 2.09 (3.17); patella length 9.30 (16.44), width 2.25 (2.82); tibia length 4.22 (7.10); tarsus length 4.00 (7.29). Leg I: femur 21.55 (47.25), patella 2.00 (2.91), tibia 39.70 (98.20), metatarsus 39.50 (89.50), tarsus 10.03 (14.51). Leg II: femur 15.60 (28.60), patella 2.06 (3.50), tibia 21.12 (33.60), metatarsus 1.47 (13.80), tarsus 2.21 (3.62). Leg III: femur 15.75 (29.40), patella 2.65 (4.45), tibia 23.48 (40.15), metatarsus 1.67 (2.53), tarsus 2.63 (3.64). Leg IV: femur 14.24 (23.50), patella 2.43 (3.83), tibia 23.30 (43.20), metatarsus 1.78 (2.65), tarsus 2.50 (3.87).

Remarks.—*Phrynus exsul* lacks the long apophysis on the pedipalpal trochanter which is a synapomorphy of *Heterophrynus*, the sole member of the Heterophryninae, and lacks the leaf-like setae on tarsus I characteristic of *Acanthophrynus*. It possesses more than three principal spines on the dorsal margin of the pedipalpal patella, which is a synapomorphy uniting *Phrynus* and *Paraphrynus* (Weygoldt 1996, 2000). These two genera are separated solely on the arrangement of the spines on the pedipalpal patella (Mullinex 1975; Quintero 1981): *Phrynus* species possess patella dorsal-3 being shorter than dorsal-2 and 4, whereas *Paraphrynus* species possess dorsal-3 and 4 being considerably shorter than dorsal-2 and 5. In this regard, *P. exsul* resembles other species of *Phrynus* but the polarity of these character states is ambiguous as the outgroup taxa

(*Acanthophrynus* and *Heterophrynus*) possess spine arrangements which do not allow for direct comparisons.

Phrynus exsul is extremely similar to other *Phrynus* species and, as noted above, the increased numbers of trichobothria on the distitibiae of legs II–IV distinguishes *Phrynus exsul* from all congeners.

Distribution.—The discovery of an Old World member of the Phrynidae poses the question of whether the species is endemic to the region or whether it may have been inadvertently introduced from somewhere in the Americas. As it represents a species that is clearly distinct from any other phrynid species (e.g., Armas 1994, 1995; Armas & Pérez 1994; Quintero 1981, 1983), it seems unlikely to represent an introduced species as any American source population would probably be already described and named. However, the disjunct distribution of the genus is highly surprising and suggests that further peculiar whip-spider species occur in Australasia.

Broadly speaking, the vast majority of the 17 currently recognized Recent whip-spider genera (Weygoldt 2000) are restricted to single biogeographic areas. *Trichodamon* Mello-Leitão 1935 (Phrynichidae), *Heterophrynus*, *Acanthophrynus* and *Paraphrynus* (Phrynidae) are restricted to the Americas. *Catageus*, *Sarax* (Charinidae), *Charon* and *Stygophrynus* (Charontidae) are restricted to Asia and Australasia. *Paracharon* Hansen 1921 (Paracharontidae), *Damon* C.L. Koch 1850, *Musico-damon* Fage 1939, *Phrynichodamon* Weygoldt 1996, *Euphrynichus* Weygoldt 1995 and *Xerophrynus* Weygoldt 1996 (Phrynichidae) are restricted to Africa. Of the remaining three genera, *Phrynichus* is found in both Asia and Africa, *Charinus*, as currently delimited, is largely circum-tropical, and *Phrynus* occurs in central America and Indonesia.

Biology.—One of the collectors of the holotype, Mr. R.E. Johnstone, informed me that several specimens of *P. exsul* were observed and all were situated on the walls in the dark zone of a cave located within limestone cliffs. Dr. Christa Deeelman-Reinhold (in litt. to Dr. Peter Weygoldt) noted that the whip-spiders were plentiful in the cave which are regarded as a tourist attraction by the local people who regard them as ‘dangerous and poisonous’, a popular misconception regarding these enigmatic arachnids. Photographs of a living spec-

imen and the entrance to the cave is provided by Weygoldt (2000, p. 131).

ACKNOWLEDGMENTS

Ron Johnstone and Ric How (Western Australian Museum) kindly collected and supplied the holotype, the identity of which was confirmed by Dr. Peter Weygoldt (Albert-Ludwigs-Universität, Freiburg). Dr. Weygoldt is also thanked for providing the paratype which was collected by Dr. Christa Deeelman-Reinhold. I also wish to thank Dr. Weygoldt, Dr. Petra Sierwald and an anonymous reviewer for their useful comments on the manuscript.

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MALE PEDIPALPAL STRIDULATORY DEVICES IN NEOTROPICAL WOLF SPIDERS AND THEIR POSSIBLE ROLE IN SYSTEMATICS

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ABSTRACT. In males of several Uruguayan lycosid species of the genera *Lycosa*, *Schizocosa*, *Aglaoctenus* and *Allocosa*, we used Scanning Electron Microscopy to investigate the existence and the morphology of pedipalpal stridulatory-like structures. These kinds of structures only appeared in species belonging to the subfamily Lycosinae, and representatives of the Allocosinae and Sosippinae subfamilies lacked them altogether. Unlike European *Lycosa* species, all surveyed Uruguayan species of the genus *Lycosa* presented the character to some extent, but interspecific differences occurred in the relative size and development of the structure. *Lycosa thorelli*, *L. carbonelli* and *Lycosa* sp. showed a very well developed pedipalpal structure, which was smaller in *Lycosa polioestoma*. *Schizocosa malitiosa* also exhibited an only partially developed structure. A possible role of these pedipalpal stridulatory-like structures in lycosid systematics is discussed.

RESUMEN. Mediante Microscopía Electrónica de Barrido, hemos analizado la existencia y la morfología de las estructuras pedipalpales de tipo estridulador en los machos de varias especies uruguayas de la familia Lycosidae (géneros *Lycosa*, *Schizocosa*, *Aglaoctenus* y *Allocosa*). Este tipo de estructuras sólo está presente en especies pertenecientes a la subfamilia Lycosinae, mientras que las especies representativas de las subfamilias Allocosinae y Sosippinae carecen por completo de ellas. A diferencia de las especies europeas de *Lycosa*, todas las especies uruguayas del género analizadas presentan la estructura, aunque existen diferencias interespecíficas en su tamaño y desarrollo relativos. *Lycosa thorelli*, *L. carbonelli* y *L.* sp. presentan una estructura pedipalpal muy bien desarrollada, mientras que su tamaño es menor en *Lycosa polioestoma*. *Schizocosa malitiosa* también posee una estructura sólo parcialmente desarrollada. Discutimos una posible aplicación de estas estructuras en la sistemática de la familia Lycosidae.

Keywords: Lycosidae, *Lycosa*, *Schizocosa*, stridulation, Scanning Electron Microscopy

The impressive number of lycosid (Araneae, Lycosidae) species reported to drum with their pedipalps or their opisthosoma during courtship interactions led to an early interest in the role of stridulation in the production of courtship vibratory signals in this family (Kronestedt 1973; Rovner 1975). The first complete description of such a structure by Kronestedt (1973) found the scraper on the fourth coxae and trochanters, and the file on the surface of the book lung opercula (type g, Legendre 1963) in *Pardosa fulvipes* (Collett 1876). He used morphological data, and interpreted the function of this structure by considering its correlation with the abdominal movements produced by males during courtship.

Most other descriptions of lycosid stridulatory devices correspond to a different location (type h), first described by Rovner (1975), where the male pedipalp bears a file on the distal tibia, facing a single crest (scraper) on the proximal tarsus. It was originally described in several *Schizocosa* and *Lycosa* species, which were known to drum with their pedipalps during courtship interactions. Morphological similarities with other species led Rovner (1975) to suggest that it could be present in most, or all, species of both genera, including non-Nearctic ones.

Rovner's prediction was later verified for *Schizocosa* (Uetz & Stratton 1982, 1983) and expanded to include Palearctic *Hogna* (*H. radiata* (Latreille 1817), Fernández-Montraveta

et al. 2000). In fact, some of the Nearctic representatives of the genus *Lycosa* originally studied by Rovner (1975) were later transferred to this second genus (*L. aspersa* to *Hogna aspersa* (Hentz 1844), *L. carolinensis* to *H. carolinensis* (Walckenaer 1805), *L. helluo* to *H. helluo* (Walckenaer 1837)). Moreover, none of the *Lycosa* species studied by Rovner (1975) remain in the genus (*L. gulosa* is now *Gladicosa gulosa* (Walckenaer 1837), *L. punctulata* is now *Rabidosa punctulata* (Hentz 1844) and *L. rabida* is now *R. rabida* (Walckenaer 1837)). European representatives of the genus *Lycosa* surveyed until now (*L. tarentula fasciiventris* Dufour 1835 and *Lycosa* sp. (Parellada 1998)) lack such a structure (Fernández-Montraveta et al. 2000). Though transferred by Roewer (1955) to the genus *Allocosa*, *L. fasciiventris* Dufour 1835 is a burrowing species. It does not share any of the characters of the subfamily Allocosinae (Dondale 1986). On the contrary, it presents the typical characters of the subfamily Lycosinae and, particularly, of the genus *Lycosa* (Zyuzin & Logunov 2000).

Kronstedt (1996) described slightly different characteristics in the corresponding structure of male *Hygrolycosa* pedipalps. The main differences concerned the direction of the grooves in the file and the shape of the scraper. He interpreted these results by considering this pedipalpal structure as an apomorphy at some supraspecific level, the distribution of the character in the family reflecting a homoplasy. We have conducted a morphological study aimed at expanding information concerning the presence and the characteristics of these kinds of structures in several Uruguayan representatives of the genera *Schizocosa* (*S. malitiosa* (Tullgren 1905), and *Lycosa* (*L. polioctoma* (C. L. Koch 1847), *L. thorelli* (Keyserling 1877), *L. carbonelli* Costa & Capocasale 1984 and *Lycosa* sp. In order to better understand the distribution of the character in the family, we additionally investigated some Uruguayan representatives of other lycosid subfamilies (Dondale 1986), particularly *Allocosa brasiliensis* (Petrunkevitch 1910) (Allocosinae), and *Aglaoctenus lagotis* (Holmberg 1876) (Sosippinae).

METHODS

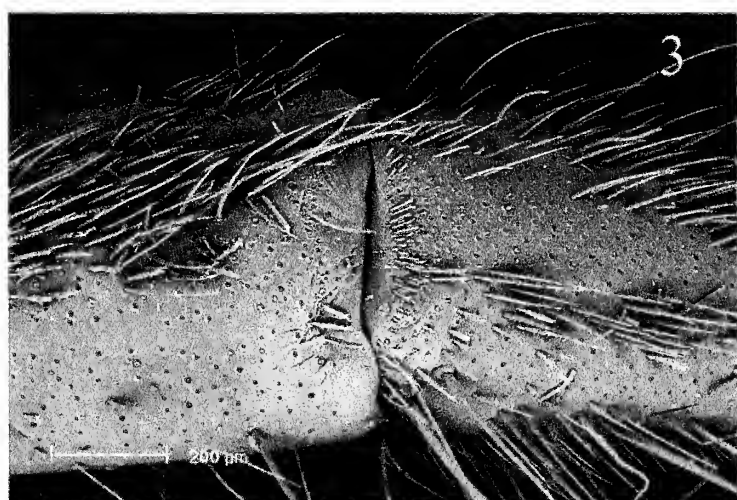
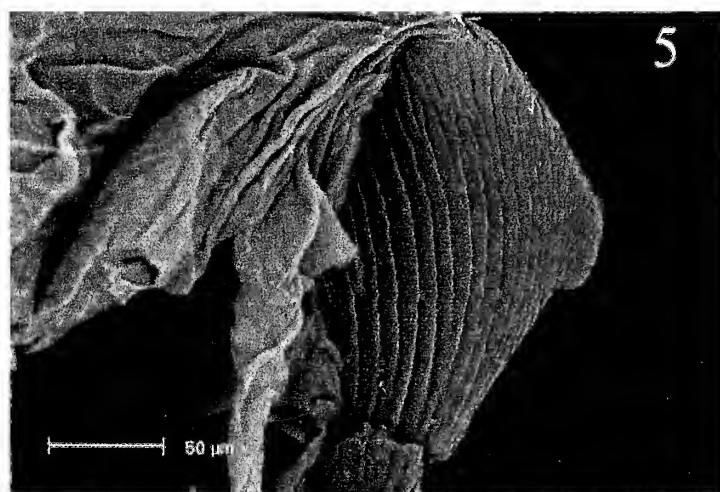
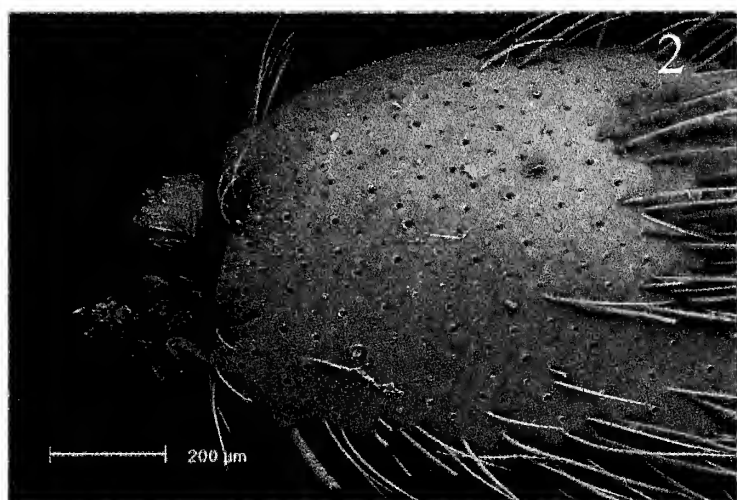
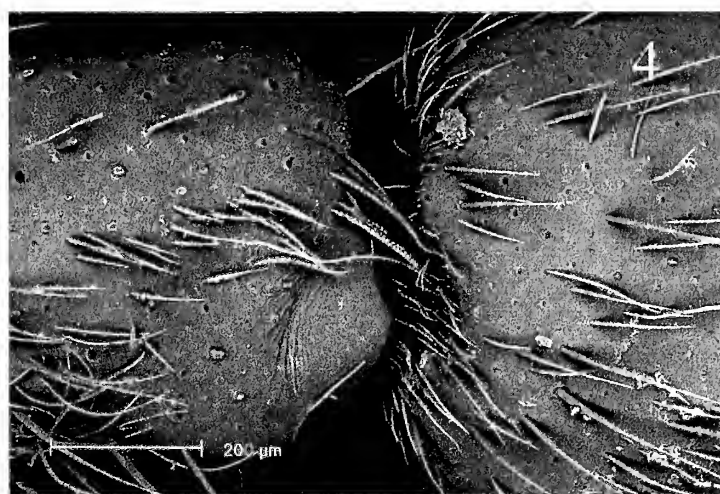
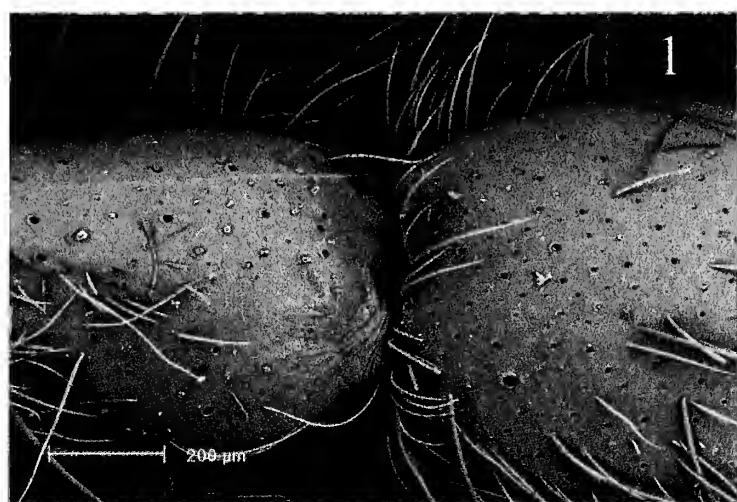
Material was prepared from adult males (one left pedipalp from two or three different

males for every species) collected in Uruguay, preserved in 70% ethanol and deposited at the collection of Sección de Entomología, Facultad de Ciencias, Montevideo. We dissected off the pedipalps and removed all hairs from the tibio-tarsal joint. One of the pedipalps was kept intact, while the tarsus of the other was separated from the tibia before dehydrating by standard procedure (ethanol series and acetone). After gold coating (BIO-RAD SC-502), samples were observed under SEM (Jeol JSM-5900LV, Servicio de Microscopía, Facultad de Ciencias, Uruguay; Philips XL30 Servicio Interdepartamental de Investigación, Universidad Autónoma de Madrid). The maximum length and width of the tibia and the tarsus was measured, together with those of the pedipalpal stridulatory-like structures. Relative sizes were calculated and compared between species.

RESULTS

The morphology of the tibio-tarsal joint of the pedipalps of *Aglaoctenus lagotis* and *Allocosa brasiliensis* are presented in Figs. 1–3. No stridulatory-like pedipalpal structure is present in any case, as no protrusion of the tibial cuticle is observed (Figs. 1, 2), nor is there any proximal crest on the tarsus (Fig. 3).

On the contrary, all representatives of the Lycosinae showed some kind of pedipalpal stridulatory-like structures (Figs. 4–16). They were always located at the prolateral margin of the dorsal tibio-tarsal joint. *Lycosa thorelli*, *L. carbonelli* and *Lycosa* sp. (Figs. 4–10) showed a well developed structure highly similar to that described for most other lycosine genera: the file in the distal tibia possessed a series of parallel grooves and the single crest on the proximal tarsus (scraper) was extremely conspicuous. Slight interspecific differences were observed in the shape of the tibial protrusion, the density of grooves and the relative size of the tarsal crest. The tibial file of *L. thorelli* occupied about two thirds of the distal tibia (Fig. 4), showed a rather limited number of corrugations (Fig. 5) and faced a scraper corresponding to 50% of the proximal tarsus width (Fig. 6). The file edge was indented, as compared to the corresponding structure in *L. carbonelli*, which was slightly higher and showed a different pattern of parallel corrugations (Figs. 7–9). Indentation also appeared in the tibial protrusion of *Lycosa* sp. (Fig. 10),



Figures 1–3.—*Aglaoctenus lagotis* (1, 2) and *Allocosa brasiliensis* (3) male left pedipalps. 1. Tibio-tarsal joint, dorsal view; tibia appears at the left; 2. Proximal part of tarsus, dorsal view; 3. Tibio-tarsal joint, dorsal view.

Figures 4–6.—*Lycosa thorelli* male left pedipalp. 4. Tibio-tarsal joint, dorsal view; tibia appears at the left; 5. Inner surface, ventral view, of the tibial protrusion, showing a set of parallel corrugations and an indented edge; 6. Proximal tarsus, dorsal view, showing the conspicuous crest (scraper) facing the tibial file.

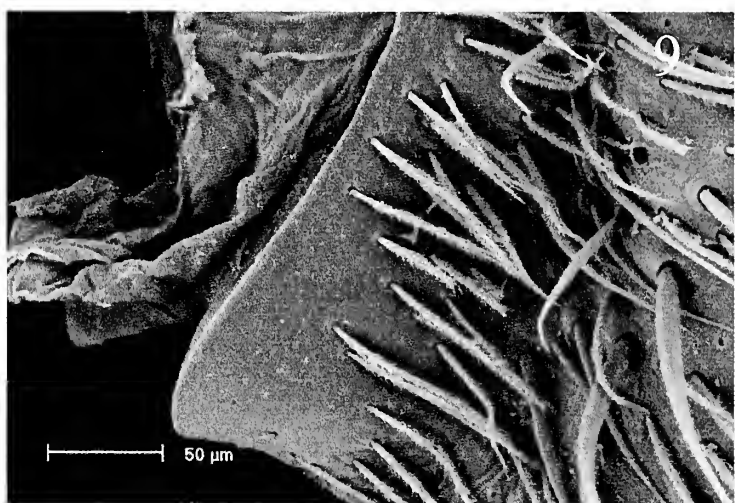
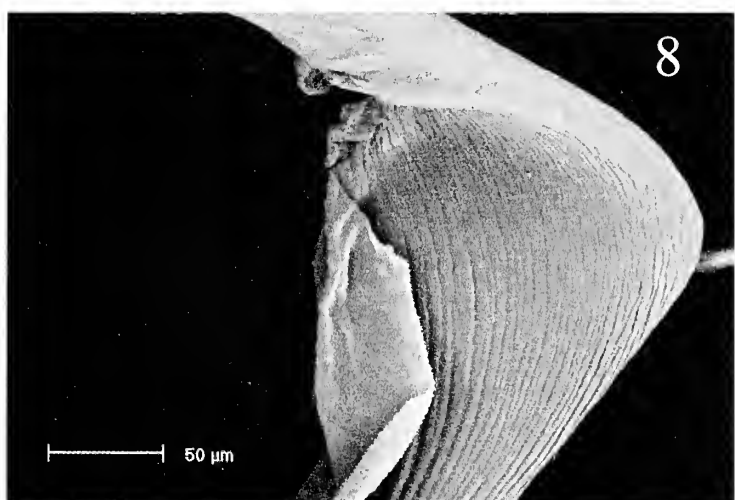
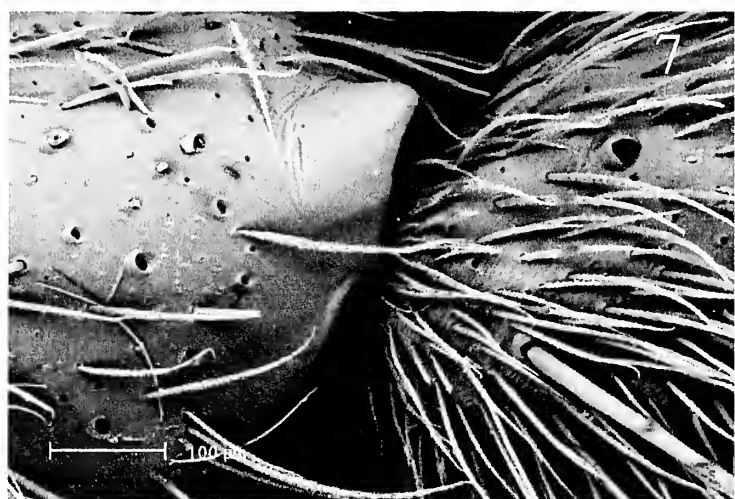
which was similar in size to the structure in *L. thorelli*.

The stridulatory-like structure found in *Lycosa poliostruma* (Figs. 11–13) was only about one third the relative size of those found in the other three species of the genus. The inner surface of the distal tibia possessed a smaller number of corrugations (Fig. 12) and the mobility of the joint was reduced. The tarsal crest was also much less conspicuous (Fig. 13), about half the relative size of those found

in the other three *Lycosa* species. A similar development of the structure appears in the representative of the genus *Schizocosa* (*S. malitiosa*, Figs. 14–16), with a smaller tibial protrusion and tarsal crest.

DISCUSSION

The morphology of the male pedipalpal tibio-tarsal joint in some Uruguayan lycosid species surveyed here only partially corre-



Figures 7–9.—*Lycosa carbonelli* male left pedipalp. 7. Tibio-tarsal joint, dorsal view; 8. Detail of the inner surface of the tibial protrusion, ventral view; 9. Proximal tarsus (dorsal view), showing the conspicuous crest (scraper) facing the tibial file.

sponds with previously published results. In contrast to some Palearctic species (Fernández-Montraveta et al. 2000), some of the Uruguayan species currently included in the genus *Lycosa* (*L. carbonelli*, *L. thorelli* and *Lycosa* sp.) possess a very well developed stridulatory-like structure. Though comparative data concerning relative sizes are unavailable, these structures strongly resemble those found in most *Hogna*, *Schizocosa*, *Gladicosa* and *Rabidosa* species (Rovner 1975; Stratton &

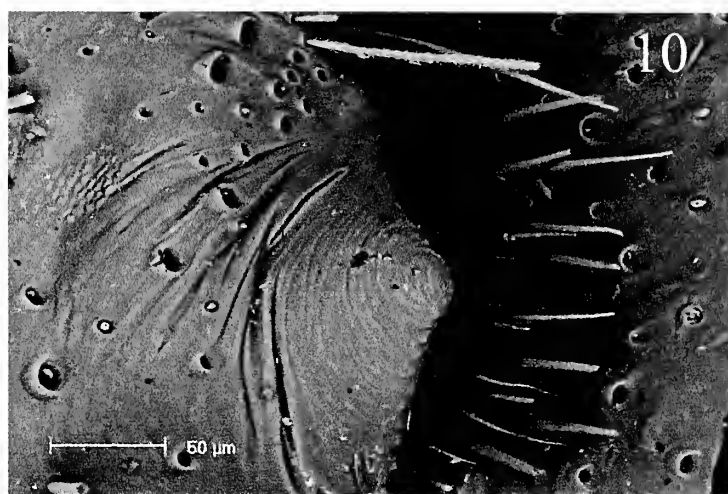
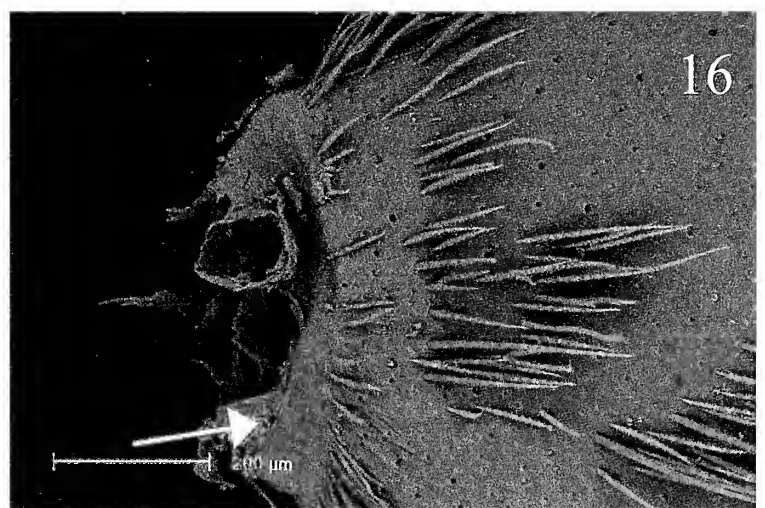
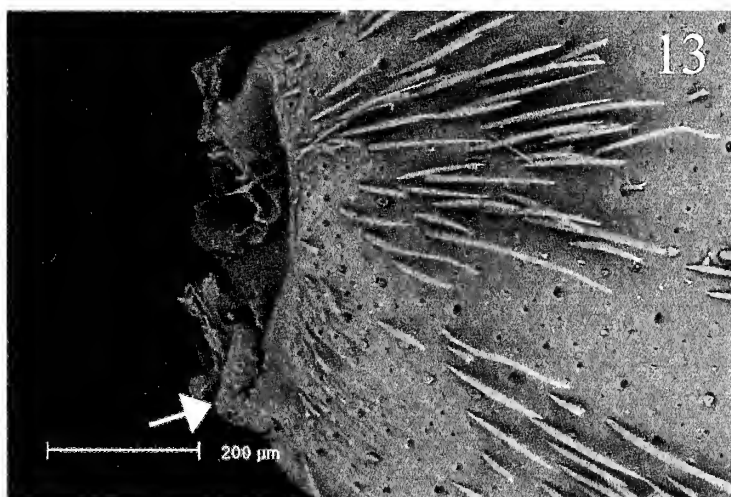
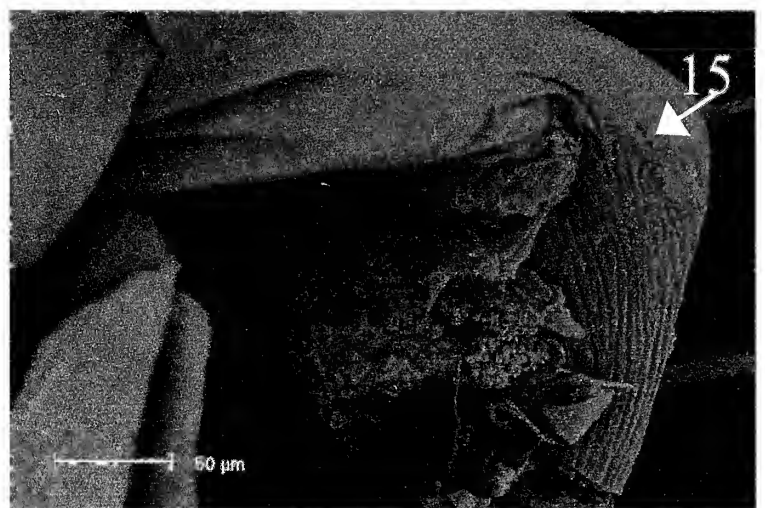
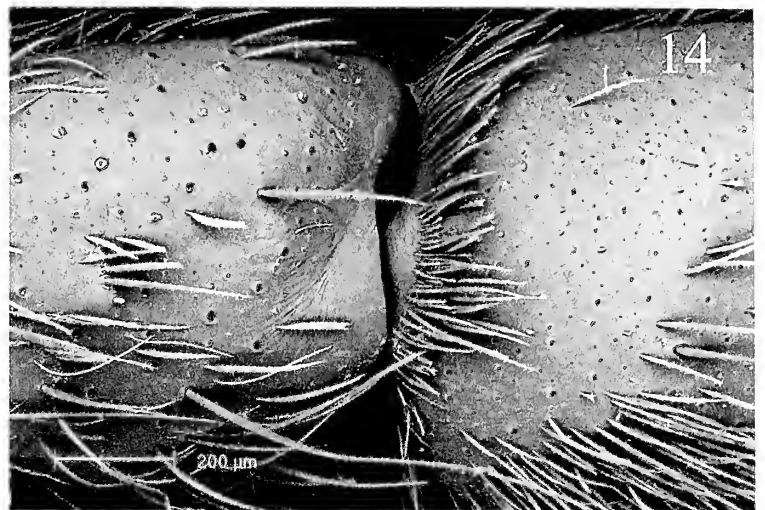
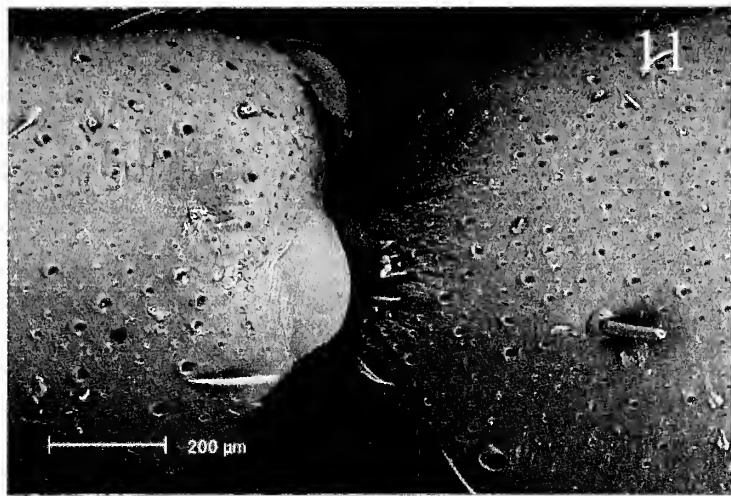


Figure 10.—*Lycosa* sp. male left pedipalp at the tibio-tarsal joint, dorsal view.

Uetz 1983; Fernández-Montraveta et al. 2000). The other Uruguayan representative of the genus *Lycosa* (*L. poliostoma*) presented a less developed structure, and was similar in this sense to the only representative of the genus *Schizocosa* (*S. malitiosa*) here studied.

This apparent inconsistency might agree with Rovner's (1975) and Kronestedt's (1996) expectations concerning the apomorphic nature of the stridulatory-like structures at a supraspecific level. First, we found no stridulatory-like structure in any of the representatives of two other lycosid subfamilies (Allocosinae and Sosippinae), nor has it ever been described in any other spider family. Second, all surveyed representatives of the Lycosinae possessed the character to some extent, and every time it was found, its position and general appearance were highly invariable. These two criteria (position and similarity) are widely accepted as useful in identifying morphological homologies in spiders (Sierwald 1989). Consequently, we hypothesize that the pedipalpal structures found in some Lycosinae are apomorphies at a suprageneric level.

This character may help solve some taxonomic problems within the Uruguayan Lycosinae, as previously stated for some Iberian species (Fernández-Montraveta et al. 2000). Thus, given the similarities in the morphology of the pedipalpal stridulatory-like structures, we hypothesize that neither *L. thorelli*, nor *L. carbonelli* nor *Lycosa* sp. should be classified as South American representatives of the genus *Lycosa*. In fact, there are some other morphological data, concerning male and female genitalia, which might support this proposal (pers. obs.).



Figures 11–13.—*Lycosa polioostoma* male left pedipalp. 11. Tibio-tarsal joint, dorsal view; 12. Inner surface of the tibial protrusion, ventral view, showing a set of parallel corrugations (arrow); 13. Proximal tarsus, dorsal view, showing the crest (arrow) facing the tibial file.

Figures 14–16.—*Schizocosa malitiosa* male left pedipalp. 14. Tibio-tarsal joint, dorsal view; 15. Inner surface, ventral view, of the tibial protrusion (arrow) showing the series of parallel corrugations; 16. Proximal tarsus, dorsal view, showing the less conspicuous crest (scraper, arrow) facing the tibial file.

As for *Schizocosa malitiosa*, the stridulatory-like apparatus is less developed than those described for other *Schizocosa* species (Rovner 1975). Moreover, it is highly similar to that found in *Lycosa polioostoma*. Interspecific similarities in other morphological (e.g. genital) characters should be analyzed in order to assess the taxonomic status of these two species. Actually, both the presence of the stridulatory-like structure and some genital

features could also question the placement of *L. polioostoma* in the genus *Lycosa*.

Besides basic similarity in placement and morphology of the stridulatory-like structures, our results also indicated slight interspecific differences. More remarkable differences occurred between the closely related species *L. thorelli*, *L. carbonelli* and *Lycosa* sp. *Lycosa thorelli* and *L. carbonelli* were originally de-

scribed as ethospecies (Costa & Capocasale 1984), given the lack of morphological differences between them. Our results might thus indicate a probable role of stridulation in the ethological isolation of these two closely related species (Stratton & Uetz 1983).

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EVIDENCE THAT THE WOLF-SPIDER *LYCOSA TARENTULA* (ARANEAE, LYCOSIDAE) NEEDS VISUAL INPUT FOR PATH INTEGRATION

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ABSTRACT. The homing behavior of *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) adult females was studied. They were tested under two conditions, diffused light (200 lux) and darkness, after having been placed in an open field. In both conditions the spiders did not orient towards the burrow position; instead, under diffused light, each spider turned at a constant angle with a value close to 135° ; this is the turn that the spider should have made in its terrarium to return to the burrow. In darkness, most of the spiders (71.4%) turned at random. In both conditions, the trajectory was roughly straight, finishing with a sudden directional change. The speed was higher under diffused light than under darkness. These results support the hypothesis that *L. tarentula* uses path integration in laboratory conditions and that it needs visual input to obtain a direction estimation in homing.

Keywords: Direction estimation, spiders, Lycosidae, *Lycosa tarentula*, vision

Most animals have a home range where they move about to find food or to locate mates. After these displacements, animals must be able to reach a spatially restricted area known to the animal: its shelter or home. Movements that enable the animal to find its shelter or home are known as homing. There are several homing mechanisms (Papi 1992), path integration being one of the most frequently used by arthropods. In path integration, the animal can return to some known point, for example, its burrow, without exteroceptive spatial information such as landmarks. While moving, the animal measures and integrates the angular changes in direction and distances traveled between each change of direction to obtain a vector whose orientation indicates home direction and whose length indicates home distance. The animal can use outward-journey information obtained through internal references, e.g., exoskeleton sense organs (Seyfarth et al. 1982; Mittelstaedt 1983; Görner & Claas 1985; Durier & Rivault 1999) or by use of external cues such as the sun or the celestial polarized-light pattern (Wehner 1997) to determine its homeward direction.

In both insects (desert ant, *Cataglyphis bicolor* (Fabricius 1793), Wehner & Srinivasan 1981; cockroach larvae, *Blattella germanica*

(Linnaeus 1767), Durier & Rivault 1999) and spiders (funnel web spider, *Agelena labyrinthica* (Clerck 1757), Moller & Görner 1994), the knowledge of distance, the other component of path integration, is expressed by a change of direction to begin a systematic search for the nest. During this search the animal returns several times to the same point while the radius of its displacement becomes greater each time.

It has been demonstrated in the funnel web spider, *A. labyrinthica* (Görner & Claas 1985), that there is an orientation change in the homeward run when the azimuthal position of a light present during this run is changed by 90° . However, the mean deviation is smaller (66° at a light intensity of 800 lux and 42° at 22 lux) than one would expect from the angular shift of the light source. This indicates that, as would be expected given that *A. labyrinthica* is a web-building spider, it does not rely exclusively on visual stimuli. Homing has also been studied in the nocturnal ctenid spider *Cupiennius salei* (Keyserling 1877) (Seyfarth et al. 1982). In this study, after having captured prey, spiders were gently chased off following either a rectilinear trajectory or a semicircular one. Seyfarth et al. (1982) demonstrated that the animal needs proprioceptive information for homing because operated an-

imals—spiders with the lyriform slit sense organs of the femur and tibia destroyed mechanically—returned with less success to the site from which they had been chased. In *C. salei*, Schmid (1997) noted differences in locomotion depending upon whether the spiders were in bright light or complete darkness.

In the lycosid spider *Lycosa tarentula* it has been demonstrated that the spider uses the celestial polarized-light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999) and that this information is gathered through the anterior median eyes which, according to Koivoo et al. (1993), have visual cells with orthogonally arranged rhabdoms. Spiders made an L-shaped outward path and then were moved to a featureless open field where they were placed at the center oriented at random. Sun position was masked by means of a screen. Under a clear sky, spiders oriented towards the burrow location relatively accurately, turning at a variety of angles to accomplish this; under an overcast sky, spiders oriented at random in the open field by turning an almost constant angle; when they could see a clear sky under a depolarizing sheet, they also oriented at random. Thus *L. tarentula* could not have used a landmark-based navigational strategy because, after the outward trip, they were moved to a featureless open field 2 m from their home terrarium and animals became oriented at random when there was no directional celestial information (sun azimuth or polarized-light pattern). In the same study, we observed (unpublished data) that under an overcast sky, spiders had a tendency to turn at a fixed angle relative to their starting direction in the open field, an angle which, in their terrarium, would have carried them near their burrows.

In this study, I describe the navigational strategy that *L. tarentula* uses in the absence of celestial cues in the laboratory and its dependence on visual information.

METHODS

Subjects.—Thirteen adult female *L. tarentula* from our laboratory stock were used. They were maintained in individual containers measuring 17 x 13 x 8 cm and they were fed mealflies (*Calliphora vomitoria* (Linnaeus 1758)) and given water twice a week.

Homing under lighting.—To begin the study of homing orientation, animals were

placed in a terrarium measuring 60 x 30 x 35 cm. This terrarium had a 15 cm deep substratum of soil; in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field. After 5 days of habituation to the terrarium, the experiment began. Spiders were gently pushed along the edge of the terrarium on a path traversing half the length and the full width of the terrarium (Fig. 1). When the spider arrived at the end of the path, it was placed into a transparent open glass container and transferred to the center of an open field 90 cm in diameter (wall height, 48 cm; visual angle, 47°). Both the terrarium and the open field were in a room without natural lighting. The room was lit in the daytime (0800–2000 h) with white light by two SYLVANIA Standard F36W fluorescent tubes producing 200 lux at the floor level of the open field. Each animal was observed 8 times and placed in one of the following compass directions at random: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°. The spider's orientation was recorded when it was at a distance of 20 cm from the center of the open field. If the spider had not moved during 20 minutes it was returned to the terrarium. The floor of the open field was thoroughly cleaned before each test.

Automated video tracking.—The image of the open field was captured by an Ikegami ICD-42B B/W CCD video camera and displayed on a Sony Trinitron color video monitor. Simultaneously, the video signal was digitized by a Targa + frame grabber that was interfaced with a personal computer supporting an object video-tracking system (EthoVision, Noldus Information Technology, Wageningen, The Netherlands). In this way, we obtained a time series of x,y positions that EthoVision used to build up the path followed by the spider during its locomotion. In the present study, the system was configured to sample the spider's location at 5 Hz.

The following parameters were determined: 1. topographic bearing of the homeward trip, 2. bearing relative to the initial orientation (α angle), and 3. displacement speed.

Homing in darkness.—Eight of the thirteen animals studied under the light condition were afterwards studied in their subjective darkness. The spiders were observed under infrared light (to which the video camera was sensitive) and under a Phillips darkroom lamp

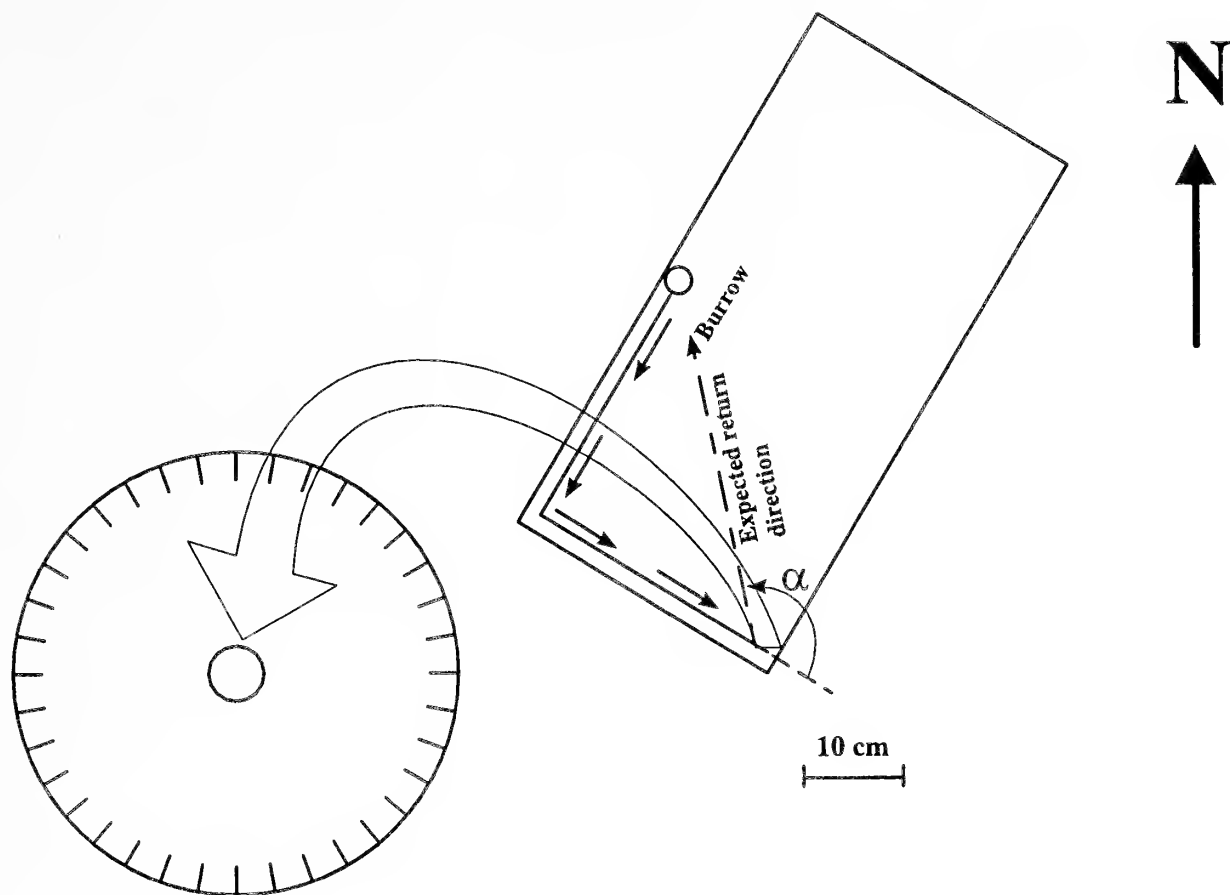


Figure 1.—Setup used to study homing in *L. tarentula*. Right, top view of terrarium in which the animal lived during the study; arrows indicate the outward path. Left, dorsal view of the open field in which the animal was left after being taken from the right corner opposite to the burrow. Burrow direction was at 350° . The big arrow indicates the transfer of the animal to the center of the open field (shown at half of its actual size in relation to the terrarium). To go to the burrow, the spider must turn an α angle of 135° in its terrarium.

so that the observer could guide the spider out of the nest. To check that the spider did not see this red darkroom light, we studied the locomotor activity cycle of four animals under an LD 12:12 cycle in which the light was supplied by the Phillips darkroom lamp. Under these conditions, the spiders showed a freerunning rhythm similar to that observed under constant conditions of darkness (DD); these results indicate that the spider cannot distinguish between the light and dark conditions of the cycle (Fig. 2). Tracking of locomotor activity under subjective darkness was carried out in a similar way to that described for homing under lighting.

Statistical analyses.—The directions followed by the animals are shown as circular distributions, which were analyzed using circular statistics (Batschelet 1981) calculating Φ (mean orientation angle) and r (length of the mean vector, ranging from 0–1). Significance was estimated using the Rayleigh test and 95% confidence limits. In order to make comparisons between the mean angles of several animals, we have used the non-parametrical Moore's test (Batschelet 1981). These statis-

tical tests have been fully described elsewhere (Ortega-Escobar & Muñoz-Cuevas 1999).

We tested the topographic bearings to evaluate whether there was an effect of distant visual landmarks or other cues on homing direction and, as there was not such an effect, afterwards we converted the topographic bearings into angles relative to the initial direction in the open field (α).

Comparisons among speeds were carried out by means of a two-factor ANOVA within-subjects design, one within-factor with two levels (light/darkness) and another within-factor with seven levels (subjects).

RESULTS

Homing under lighting.—Paths followed by the spiders in the open field were roughly straight, finishing with a sudden turn either to the right or to the left, followed by a turn in the opposite direction (Fig. 3).

This series of turns has also been observed when the animal is taken from the burrow without having been displaced and transferred to the center of the open field. This type of

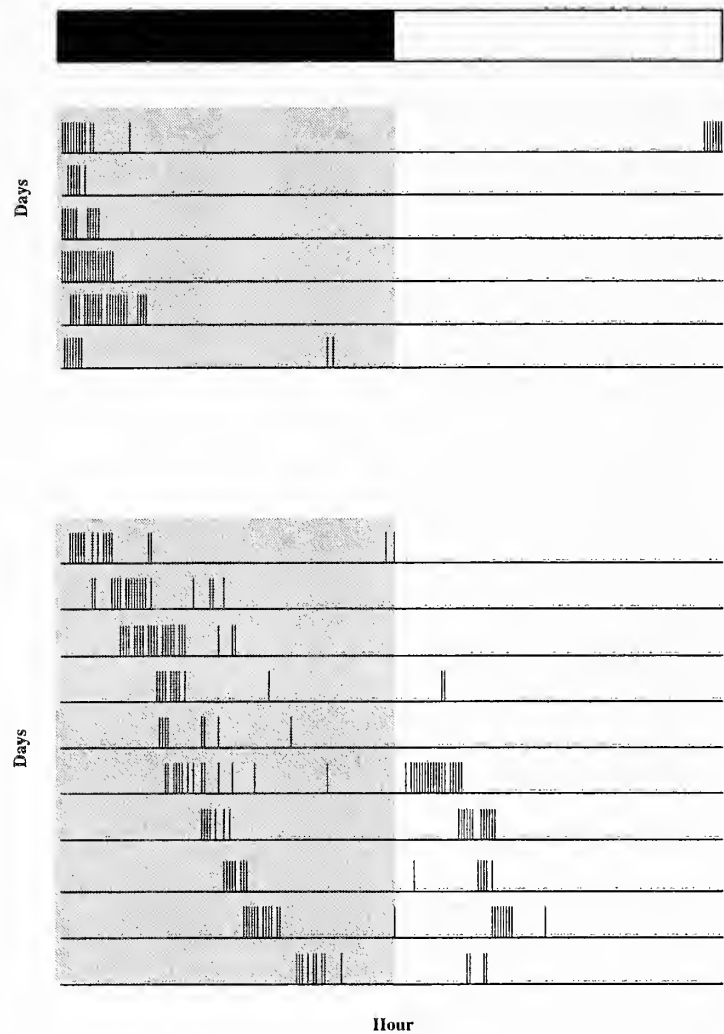


Figure 2.—Top: Locomotor activity rhythm of an animal submitted to a LD cycle 12 (white light):12 (darkness); it can be observed that the locomotor activity is adjusted to the LD cycle. Bottom: Locomotor activity rhythm of an animal submitted to a LD cycle 12 (red light):12 (darkness); it can be observed that locomotor activity is freerunning.

behavior has been called systematic search and we have not analyzed it in this study.

Some spiders defecated in the open field before homing; in order to do this they walked backwards a variable distance, generally never less than 5 cm, defecated, and then began homing. We have not used these paths in our analysis.

None of the 13 spiders used in this experiment oriented towards the burrow or towards another point of the room in a constant way in the eight tests (Fig. 4a). However, α was non-randomly oriented in 12 of the 13 animals (Fig. 4b). The mean vectors of these 12 animals were not statistically different (Moore's Test: $D = 1,512$, $P < 0.05$).

Homing in darkness.—The homeward paths of these animals were very similar to those observed under lighting: they were roughly straight, finishing by systematic searching. The topographic bearings (Fig. 4c) have a random orientation except in one ani-

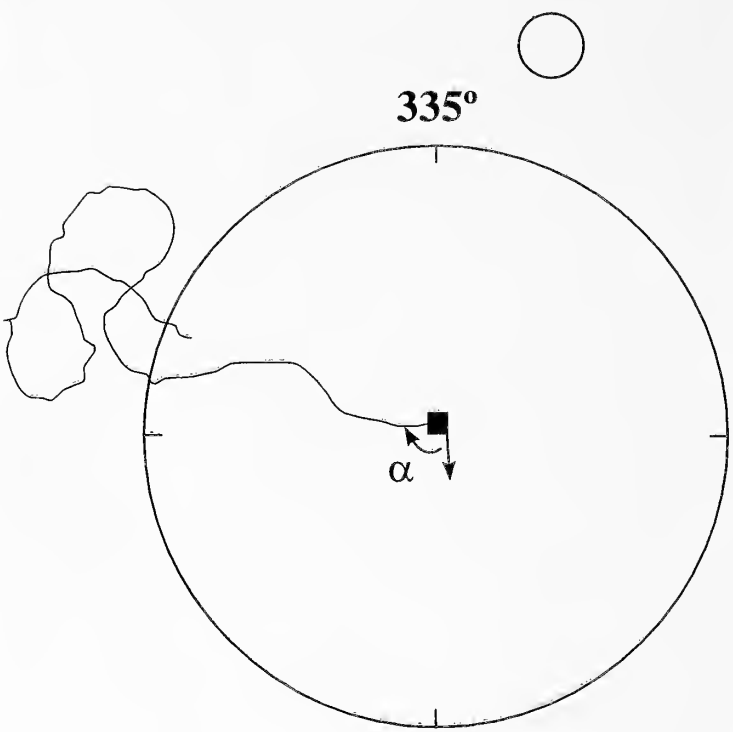


Figure 3.—Example of a homing path in the open field under lighting. The black square in the center represents the point where the spider is placed and her orientation is indicated by the arrow; the little circle represents the burrow compass direction. α is the angle between the initial orientation and final bearing.

mal. The angle α (Fig. 4d) has also a random orientation in five (71.4%) of the seven animals. There are only 7 vectors under the darkness condition because one of the animals did not walk in any of the 8 tests.

Comparisons of the speed in both conditions.—The mean velocity for all the subjects under lighting was $2.03 \pm 0.31 \text{ cm}\cdot\text{s}^{-1}$; the mean value for all the subjects in darkness was $0.93 \pm 0.10 \text{ cm}\cdot\text{s}^{-1}$. ANOVA revealed a significant effect of lighting on the velocity along the homeward path, $F_{(1,7)} = 10.487$, $P = 0.014$, while there were no differences between subjects, $F_{(6,42)} = 1.313$, $P = 0.273$ and the interaction of lighting condition vs. subjects was not significant, $F_{(6,42)} = 1.654$, $P = 0.156$.

DISCUSSION

Our results show that, during the day, *L. tarentula* does not orient towards the topographic burrow position under the experimental conditions of the absence of tacto-chemical information and the presence of distant visual landmarks of the laboratory. Inside the open field the animal could still use 50° of the visual field of the posterior median eyes or the posterior lateral eyes (Land 1985) to see distant visual landmarks. Nonetheless, the spider

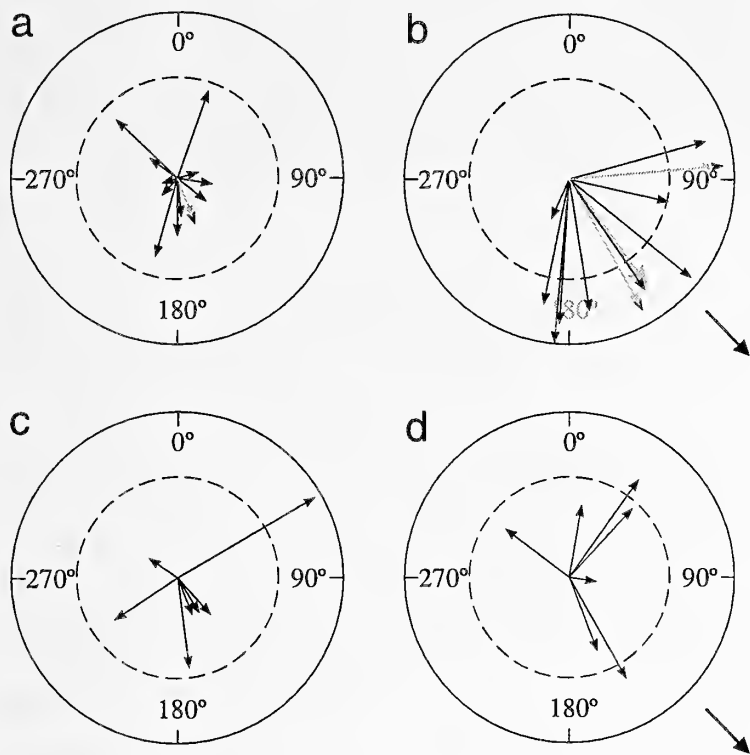


Figure 4.—a. Mean vectors of the topographic bearings of the animals studied under the light condition. Burrow direction is at 350°. The dashed circle indicates the critical r -value of $P = 0.05$. b. Mean vectors of α (the angle of movement relative to the initial orientation in the open field) of the animals studied under the light condition. The thick gray arrow represents the mean vector of all the animals ($\alpha = 144^\circ$). 0° indicates that the animal looks for home in the same direction as its initial orientation in the open field. The external arrow represents the angle the spider must turn to, in effect, go back to the burrow ($\alpha = 135^\circ$). c. Mean vectors of the topographic bearings of the animals studied under dark condition. d. Mean vectors of α of the animals studied under the dark condition.

did not orient towards its burrow. These results are in agreement with what has been observed when the animals could use neither the sun nor the polarized light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999). In contrast, under diffuse non-polarized light, *L. tarentula* try to return home by turning a fixed angle, $\alpha \sim 135^\circ$. A turn of 135° would let the animal walk to a point near the burrow if the spider's orientation had not been changed in the open field. Although systematic observations were not made in the terrarium, some animals that showed $\alpha \sim 135^\circ$ in the terrarium, also showed it in the open field and something similar was found for those with $\alpha \sim 180^\circ$.

To obtain the appropriate α , spiders could use either idiothetic information, visual information or a combination of both. Idiothetic information was the same in both experi-

ments; however, during the day but in darkness, path integration fails to provide a correct estimate of α (Fig. 4d). In another diurnal arthropod, the bumblebee (*Bombus impatiens* (Cresson 1863)), it has also been shown that path integration fails to provide a correct estimate of home direction when bees cannot use visual information (Chitka et al. 1999). So, it seems necessary that some kind of visual input be perceived during the outward path in order to achieve or activate path integration. In the wild and during the day, *L. tarentula* females walk out from their burrows only when there is prey or another conspecific, while in the night (natural darkness) they walk out spontaneously without the presence of prey or conspecifics. This different behavior must also be based on some differences between day and night eye states and the visual fields of the different eyes. I think that *Lycosa tarentula* activates path integration by using proprioceptive information and visual information gathered by the anterior lateral eyes (ALE) which have ventral visual fields whose images change very little when the animal walks in comparison with the images on the anterior median (AME), posterior median (PME) or posterior lateral eyes (PLE) that move quickly given their visual fields. In this way, it is easiest to make an association between the proprioceptive information and the visual information generated by the ALEs.

Our results contrast with those on *Cupiennius salei* (Seyfarth et al. 1982); in that study the animals could not use visual information because their eyes were masked, but they were capable of returning to the point from which they had been chased by using only proprioceptive information supplied by the lyriform organs. In addition, during their walks in darkness, *Cupiennius* (Schmid 1997) use exploratory movements of the first pair of legs, a kind of behavior that we have not observed in *L. tarentula*.

With our data we cannot analyze how *Lycosa tarentula* carries out distance estimation because although the distance that it should walk to the burrow was near 36 cm and the radius of the open field was 45 cm, there were many trials in which the animal walked as far as the open field wall and then followed it.

Walking speed is greater in the light than in the dark. Because there are no other differences in the linear aspect of the paths, that

difference seems to indicate again that *L. tarentula* needs some kind of visual information perceived during the outward trip to integrate the homeward one. In other walking arthropods, it has been observed that walking speed is lower when they cannot use ventral optic-flow cues (desert ant, *Cataglyphis fortis*, Ronacher & Wehner 2000). *Lycosa tarentula* could use a similar mechanism because it walks the same distance, 20 cm, at a higher speed under light, in the presence of self-induced optic flow, than in darkness, when there is not such information.

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THE OLDEST LINYPHIID SPIDER, IN LOWER CRETACEOUS LEBANESE AMBER (ARANEAE, LINYPHIIDAE, LINYPHIINAE)

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ABSTRACT. A new fossil Linyphiidae: Linyphiinae is described from 125–135 Ma old (Upper Neocomian–basal Lower Aptian) Cretaceous amber from the Kdeirji/Hammana outcrop, Lebanon. This is the oldest known linyphiid as well as the oldest described amber spider. The first major radiation of the linyphiid subfamilies occurred in the early Cretaceous, if not before, and the presence of Linyphiidae in this period predicts the presence of Pimoidae then too. Current evidence, which suggests the higher araneoids did not radiate and diversify until after the end-Cretaceous mass extinction event may be an artefact of sample size.

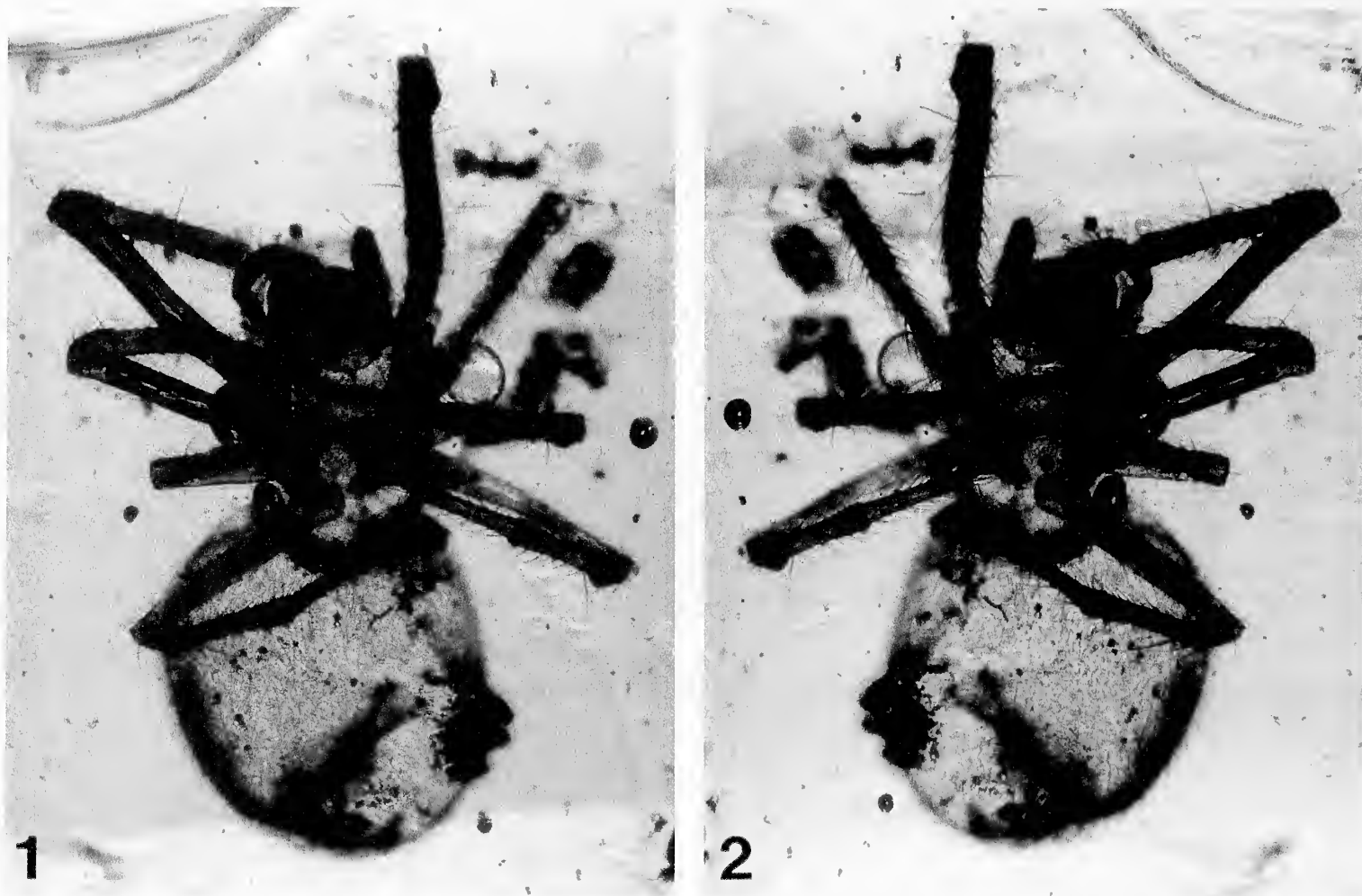
Keywords: Linyphiidae, Linyphiinae, Lebanese amber fossil

The spider family Linyphiidae contains 4,129 extant species in 550 genera (Platnick 2001), which represents approximately nine percent of total spider species diversity. It ranks second, after Salticidae, in terms of number of described species, but first for number of genera (Platnick 2001). However, many of these genera are monotypic and would probably not withstand phylogenetic scrutiny (Hormiga 2000). The family consists mainly of very small spiders, mainly sheet-web builders. It has a global distribution, but linyphiids are most diverse in northern temperate regions (Coddington & Levi 1991). Their niche may be occupied by Theridiidae in the lower and southern latitudes (e.g. Nentwig 1993: table 8). There are six recognized extant linyphiid subfamilies: Dubiaraneinae Millidge 1993, Erigoninae Emerton 1882, Linyphiinae Blackwall 1859, Micronetinae Hull 1920, Mynogleninae Lehtinen 1967, and Stemonyphantinae Wunderlich 1986 (A. Tanasevitch pers. comm.), although the Linyphiinae are considered by some (e.g. Hormiga 2000) to consist of two tribes: Micronetini and Linyphiini, reducing the number to five (e.g. Hormiga 1994a, 2000).

Fossil linyphiids have been described from Tertiary ambers from the Dominican Republic (Miocene, 15–20 Ma) (Wunderlich 1988), Mexico (Miocene–Oligocene, 19–27 Ma) (Petrunkévitch 1971), the Baltic region (Eocene, 44 Ma) (Petrunkévitch 1942, 1958; see also

taxonomic comments of Wunderlich 1986) and from Upper Cretaceous (Turonian, 90–94 Ma) amber from New Jersey (Penney in press). Wunderlich (1998) described a linyphiid from what was thought to be Dominican Republic amber, but has since been shown to be Madagascan copal (J. Wunderlich, pers. comm.), which is semi-fossilized resin less than two million years old. A non-amber fossil linyphiid was described by Berland (1939) from the Oligocene of Alsace, France. The specimen in Mexican amber is an exuvium from an immature spider, and the French specimen is poorly preserved. Both were described and named as linyphiids, but we consider their current placement in the Linyphiidae to be unreliable. Fossil linyphiids have been reported as present, but not described, from Eocene Bitterfeld amber (44 Ma) (Schumann & Wendt 1989) and Upper Cretaceous Canadian amber (65–83 Ma) (McAlpine & Martin 1969).

This paper describes the oldest known linyphiid spider from upper Neocomian–basal Lower Aptian (c. 125–135 Ma) Cretaceous Lebanese amber from the Kdeirji/Hammana outcrop, which represents one of the oldest insect inclusion-bearing amber deposits (Azar 1998). This specimen is the oldest described amber spider, the previous being a new genus and species of Nemesiidae described in Barremian amber from the Isle of Wight, UK (Selden in press).



Figures 1–2.—Female linyphiine in Lebanese amber, photomicrographs of holotype. 1. Dorsal view x50; 2. Ventral view x50.

METHODS

Preservation.—The spider is preserved in a very small piece (3 x 3 x 1 mm) of clear, yellow-colored amber. There are a few air bubbles of varying size and a small number of organic and inorganic syninclusions.

Methods.—The amber piece had been prepared by being set in a clear synthetic resin disc (22 mm diameter x 2 mm thick), and polished prior to receipt by the authors. The specimen was studied, drawn and photographed, using both transmitted and incident light, using a Nikon Optiphot stereomicroscope, with a camera lucida drawing tube and a Nikon FX-35DX camera attached by means of a phototube. An Olympus SZH stereozoom microscope with incident light revealed additional detail of the specimen. All measurements are in mm.

Abbreviations used in the text and figures.—ab = air bubble; at = anal tubercle; ch = chelicera; co = colulus; cx = coxa; ep = epigyne; fe = femur; la = labium; mx = maxilla; mt = metatarsus; op = opisthosoma; pa = patella; pp = pedipalp; sp = spinneret; st = sternum; ta = tarsus; ti = tibia; tr = trichobothria; 1–4 = walking legs 1–4. In the

leg formula (e.g. 4123), the legs are ranked in order of length (longest first). Tm1 and Tm4 are measurements of the distance that a trichobothrium is located along the lengths of metatarsi 1 and 4 respectively, relative to the length of the leg segment, e.g. Tm1 = 0.3 indicates that the trichobothrium is located three tenths of the way along metatarsus 1, from the proximal end of the segment.

SYSTEMATIC PALAEONTOLOGY

Family Linyphiidae Blackwall 1859
Subfamily Linyphiinae Blackwall 1859
gen. et sp. indet.
Figs. 1–3

Distribution.—Upper Neocomian–basal Lower Aptian (c. 125–135 Ma) Cretaceous Lebanese amber from the Kdeirji/Hammana outcrop, Lebanon.

Only known specimen.—Female, specimen No. 491 preserved in Cretaceous Lebanese amber, held in the Laboratoire d'Entomologie, Muséum National d'histoire Naturelle, Paris (MHNP), examined.

Description.—*Measurements:* body length 1.86; carapace ground away (Fig. 1), but the

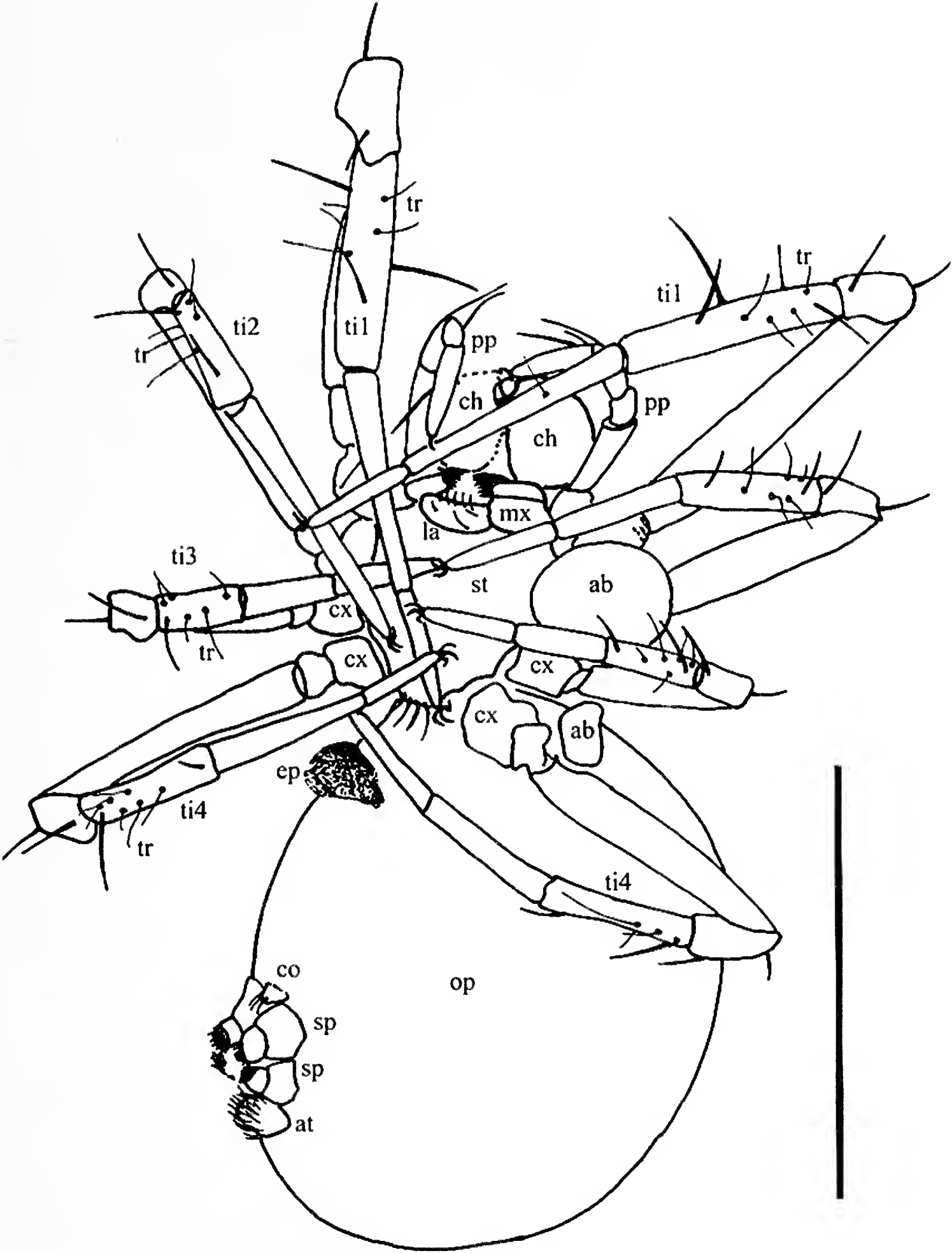


Figure 3.—Female linyphiine in Lebanese amber, camera lucida, ventral view. Scale bar = 1 mm.

chelicerae are in place so it is possible to determine the body length. Detailed structure and dentition of chelicera are not visible, but it appears unmodified and lacks stridulatory striae on the ectal surface. Maxilla wider than

long with distinct serrula and a transverse row of dark, chitinized denticles; labium slightly rebordered, much wider than long. Sternum 0.43 long, 0.40 wide, smooth, with sparse covering of setae; margin slightly incised to

accommodate coxae, sharply truncated posteriorly where it extends between fourth coxae; five erect setae along the truncated edge. Opisthosoma 1.23 long, 1.00 high, sub-spherical, without tubercles or scuta, covered with short setae; the right side has collapsed inwards. Anterior lateral and posterior lateral spinnerets with numerous spigots, posterior median spinnerets not visible. Colulus relatively large, with at least three bristles. Anal tubercle distinct (Figs. 2, 3). Epigyne projects ventrally, appears domed in lateral view (a clear ventral view is not possible because of the position of the spider in the amber matrix so the detailed structure is not clear). Epigyne heavily sclerotized, with a single opening and a flat dorsal margin; lateral margins appear rounded and project slightly posteriorly.

Leg formula 1423. Leg 1 fe 0.71, pa 0.19, ti 0.43, mt 0.41, ta 0.33, total 2.07; leg 2 fe 0.57, pa 0.16, ti 0.29, mt 0.26, ta 0.24, total 1.52; leg 3 fe 0.41, pa 0.14, ti 0.21, mt 0.19, ta 0.17, total 1.12; leg 4 fe 0.63, pa 0.16, ti 0.33, mt 0.31, ta 0.21, total 1.64; all segments with distinct setae and annulate distally. Coxae and trochantera without modifications; fe 1 and possibly fe 2 with short median dorsal spine, apparently lacking on fe 3 and 4; fe 1 with long prolateral spine located just distal to midpoint; all patellae with proximal and distal dorsal spines; tibial spination 2, 2, 2, 2; ti 1 also with median, long prolateral spine; metatarsi and tarsi without spines (Figs. 1–3). All tibiae with trichobothria equal to or longer than the tibial diameter (Fig. 3); Tm1 = 0.3, Tm4 lacking. Tarsi with three simple, untoothed claws and accessory setae, unpaired claw long, pedipalp with a single simple claw.

Remarks.—It is well appreciated that amber spiders are taxonomically subequal to Recent spiders (e.g. Eskov 1990). In many fossils it is difficult to identify and study those characters considered important as diagnostic for extant taxa. The specimen described here cannot be diagnosed by any putative autapomorphies, so a specific epithet is not assigned, nor can it be placed with certainty in an extant

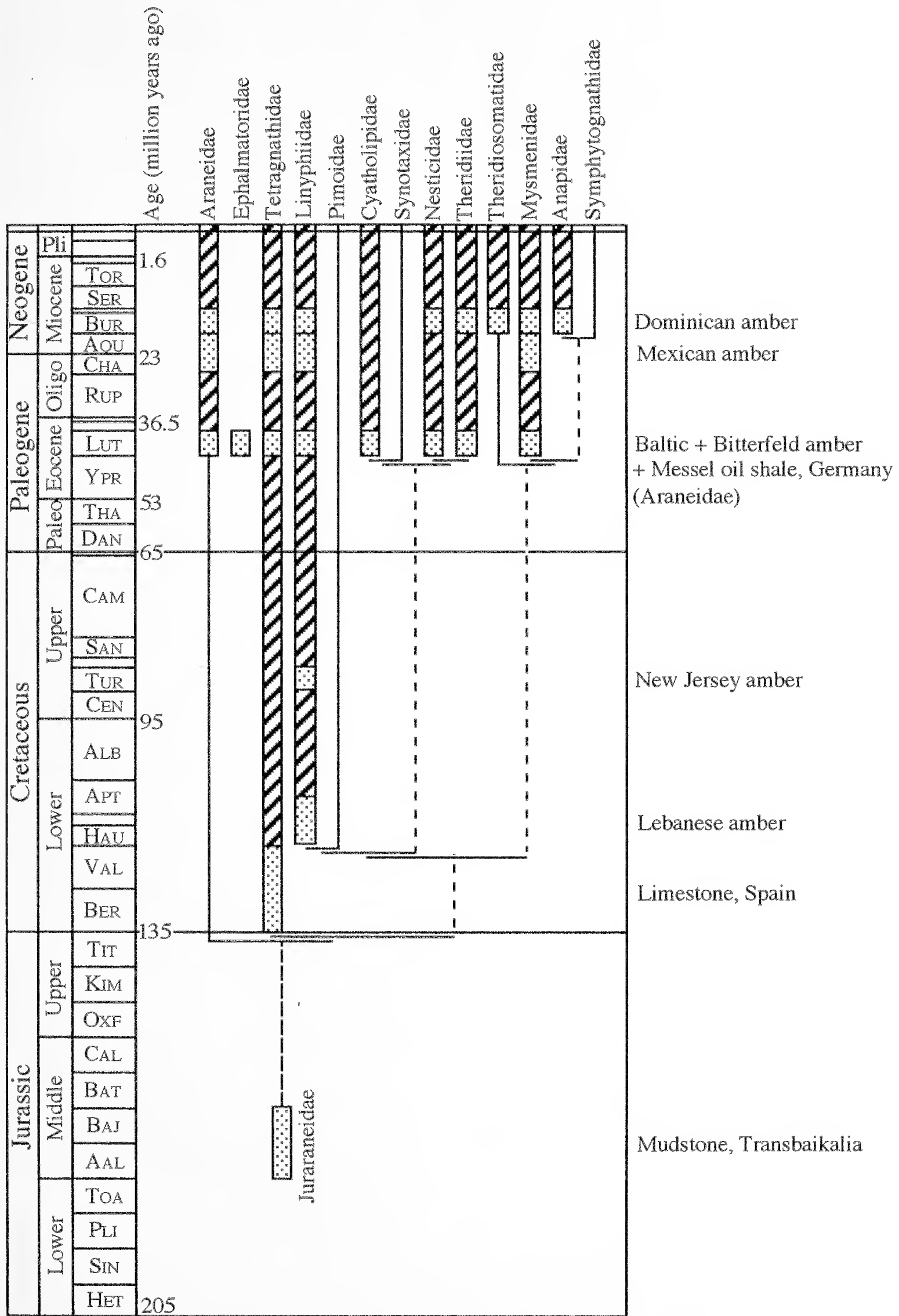
genus. This female linyphiine, it is the oldest representative of the Linyphiidae recorded, and is also the oldest described amber spider.

DISCUSSION

The superfamily Araneoidea comprises twelve extant families (Griswold et al. 1998) and the extinct families Ephalmatoridae Petrunkevitch 1950, redefined by Wunderlich (1986) from Baltic amber, and Juraraneidae Eskov 1984 from the Jurassic of Kazakhstan. The phylogenetic scheme for the Araneoidea (Fig. 4) follows Griswold et al. (1998), except for the placement of the fossil taxa. According to Griswold et al. (1998) the unambiguous synapomorphies for the linyphioid families, which includes Linyphiidae and its sister taxon Pimoidae (see Hormiga 1994b), are stridulating striae ectally on the male chelicerae, patella–tibia autospasy, and an enlarged base on the basal posterior lateral spinneret cylindrical gland spigot. The fossil specimen is female, all legs are intact, and the fine detail of the spigots is not clear. The fossil is excluded from the Pimoidae on account of its size, considerably smaller than 5 mm, the lower end of the range given by Hormiga (1994b), the epigyne does not protrude posteriorly beyond the epigastric furrow as it appears to in many pimoid species, femur 4 lacks dorsal spines, and the legs lack long setae which are curved at their distal end (e.g. Hormiga 1994b). The systematic placement of many genera within linyphiid subfamilies is based solely on autapomorphies derived from male secondary genital organs and in some cases no unambiguous diagnostic character states have been established for female specimens. Therefore, we tentatively place this specimen in the Linyphiidae: Linyphiinae, based on the remaining somatic and genitalic morphology, for example the legs spination and trichobothrial patterns, but to which tribe (Micronetini or Linyphiini) it belongs is uncertain. We accept that this placement is not based on any putative autapomorphies and are unaware of any studies, which provide reliable diagnostic or phy-

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Figure 4.—Evolutionary tree of the Araneoidea. Dotted fill = described fossil, striped fill = known geological range, vertical solid lines = range extension, horizontal solid lines = phylogenetic relationships, tight dashed lines = ancestral lineage, loose dashed lines = ghost lineage, Lagerstätten on right side. Terminology follows Smith (1994).



logenetic chaetotaxy or trichobothrial patterns. However, paleoarachnologists are often confronted with fossils which are unique and do not possess, or clearly exhibit, the characters used in Recent spider taxonomy and systematics, but important specimens of great antiquity such as this warrant description and placement as far as is possible.

The presence of fossil Linyphiidae in the upper Neocomian–basal Lower Aptian (c. 125–135 Ma) predicts the presence of Pimoidae, otherwise unknown in the fossil record, in the Cretaceous. It also predicts the occurrence of the spineless femur clade and the symphytognathoids, or their ancestors approximately a further 35 Ma back in the fossil record, from the oldest known described fossil Linyphiidae in Turonian New Jersey amber (Penney in press) (Fig. 4). A number of authors e.g. Wunderlich (1986), Millidge (1993) and Hormiga (1994a, 2000) have provided various hypotheses regarding the subfamilial phylogenetic relationships within the Linyphiidae. These were compared and contrasted by Hormiga (2000) whose favored cladogram had the Linyphiinae (Micronetini and Linyphiini) as a sister group to the remaining linyphioid taxa, excluding Millidge's (1993) Dubiaraneinae, which Hormiga considered a dubious taxon. However, it remains to be seen whether these proposed relationships withstand future phylogenetic analyses incorporating more linyphiid species and more character states (Hormiga 2000). Accepting Hormiga's (2000) cladogram, which can be represented in parenthetical notation as: (((((Stemonyphantinae) (Mynogleninae)) (Erigoninae)) ((Micronetini) (Linyphiini))))), as the most reliable indication of the intrafamilial phylogeny currently available, then this fossil is direct evidence that the first major radiation, which separated the Linyphiinae from the remaining linyphiid taxa, occurred in the early Cretaceous, if not before.

The current fossil evidence (Fig. 4) gives the impression that the more derived, higher araneoids radiated and diversified in the Tertiary after the end-Cretaceous mass extinction event. However, we suspect that this observation is a sampling artefact. Thousands of Tertiary amber spiders, particularly from the Baltic and the Dominican Republic, have been studied over the last century and a half, whereas probably fewer than 50 specimens of

Cretaceous spiders, many of which are poorly preserved and not identifiable to family, account for the only three publications to date (Eskov & Wunderlich 1994; Penney in press; Selden in press) that describe Cretaceous amber spiders. The relatively large number of Recent spider families being discovered in rocks and amber of Mesozoic age suggests a great antiquity of modern spider families (Selden & Penney 2001), we would expect to find some of these families given enough Cretaceous specimens and are currently working through this material.

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ESTIMATING THE STICKINESS OF INDIVIDUAL ADHESIVE CAPTURE THREADS IN SPIDER ORB WEBS

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ABSTRACT. Sticky threads improve an orb web's ability to retain the insects that strike it, allowing a spider more time to subdue these insects before they can escape from the web. The adhesive capture threads found in most orb webs feature small droplets of aqueous material. Inside each droplet, glycoprotein granules coalesce to impart thread stickiness. An independent contrast analysis of threads produced by the adults of five species (*Leucauge venusta*, *Argiope trifasciata*, *Micrathena gracilis*, *Cyclosa conica*, *Araneus marmoreus*) and ontogenetic studies of the threads of two of these species show that the volume of material in a thread's droplets is directly related to its stickiness. Models based on these analyses predict thread stickiness to within an average of 11% of the mean measured values using measurements of droplet diameter and distribution that are easily made with a compound microscope. This approach will facilitate the inclusion of thread stickiness in studies that examine the properties and performance of spider orb-webs.

Keywords: Araneae, orb web, prey capture, spider thread, stickiness

The spirally-arrayed capture thread of a spider's orb web retains insects that strike the web, giving the spider more time to subdue these prey before they escape from the web (Chacón & Eberhard 1980; Eberhard 1986, 1989, 1990). Orb weaving spiders belong to the Orbiculariae clade, which is comprised of two subclades: the Deinopoidea, whose members produce primitive cribellar capture threads, and the much larger Araneoidea, whose members produce viscous capture threads (Bond & Opell 1998; Coddington 1986, 1990a, 1990b; Coddington & Levi 1991; Griswold et al. 1998). Cribellar threads are dry fuzzy threads in which the outer surfaces are formed of thousands of fine, looped fibrils that are spun from the spigots of a spinning plate termed the cribellum and, in the Deinopoidea, are supported by a pair of inner axial fibers (Eberhard & Pereira 1993; Opell 1994a, 1994b, 1995, 1996, 1999a; Opell & Bond 2001). These cribellar fibrils snag on the setae and irregular surfaces of insects and adhere to smooth surfaces by van der Waals and hygroscopic forces (Opell 1994c; Hawthorn & Opell pers. obs.). In contrast, the viscous capture threads of araneoids are formed of a pair of supporting axial fibers overlain by a complex aqueous solution that coalesces into regularly spaced droplets (Vollrath 1992; Vollrath

et al. 1990). Within each droplet, a glycoprotein granule condenses and confers the thread's stickiness (Peters 1995; Tillinghast et al. 1993; Vollrath & Tillinghast 1991). Relative to both spider size and capture thread volume, viscous thread is stickier than cribellar thread (Opell 1997, 1998). Consequently, araneoids construct orb-webs with a greater stickiness per capture area than do deinopoids (Opell 1999b).

The stickiness of adhesive capture threads differs greatly among species and is related to both spider mass and web architecture (Opell 1997, 1998, 1999b). Although few in number, studies that have examined the effect of thread stickiness on orb web performance have found it to be significant. Using artificial orb web analogs, Chacón & Eberhard (1980) showed that increasing the amount of adhesive on the lines of these "webs" increased the number of prey that they retained. The observation that orb webs constructed by adult spiders retained prey for longer periods than those of conspecific juveniles was attributed to the putatively stickier threads produced by adults (Eberhard 1989), as was the greater size of prey captured by adults (Opell 1990). Using measurements of capture thread stickiness, capture thread length, and web capture area, Opell (1997, 1999b) computed and compared

the total stickiness and the stickiness per capture area of orb webs constructed by several species. However, ecological studies of orb web performance have never incorporated thread stickiness. This is because the techniques for measuring stickiness have only recently been developed and are rather laborious (Opell 1997, 1998).

Because glycoprotein granules condense from the material that forms a thread's droplets, I hypothesize that droplet volume is directly related to thread stickiness. Phylogenetic analysis of adhesive threads produced by five species and ontogenetic analyses of the threads produced by two of these species support this hypothesis. Formulas derived from these analyses make it possible to estimate accurately the stickiness of adhesive capture threads using a simple set of measurements made with a compound microscope. This procedure thus makes estimates of the stickiness of individual threads accessible to ecological and comparative studies.

METHODS

Species studied.—I selected for study five species that represent major araneoid clades (Fig. 1), show considerable ecological diversity, and were abundant enough near Blacksburg (Montgomery County), Virginia to permit the sample sizes required by my studies. These species were identified using the systematic studies of Berman & Levi (1971) and Levi (1968, 1976, 1977, 1980, 1985). Voucher specimens are deposited in the Museum of Comparative Zoology, Harvard University. One value for droplet volume and one value for thread stickiness were computed from the threads produced by each spider. Interspecific comparisons are based on threads produced by adult females.

Leucauge venusta (Walckenaer 1841) is member of the family Tetragnathidae. Adult females have a mean body mass of 28.1 mg ($n = 26$, $SE = 2.3$), are typically found in shaded forest edges, and construct horizontal orb webs. The remaining species are members of the family Araneidae. *Argiope trifasciata* (Forskål 1775) is a large orb-weaver with a mean adult female body mass of 474.0 mg ($n = 25$, $SE = 51.6$). It is found on weedy vegetation, typically in exposed areas, where it constructs vertical orb webs with widely spaced capture spirals. *Micrathena gracilis*

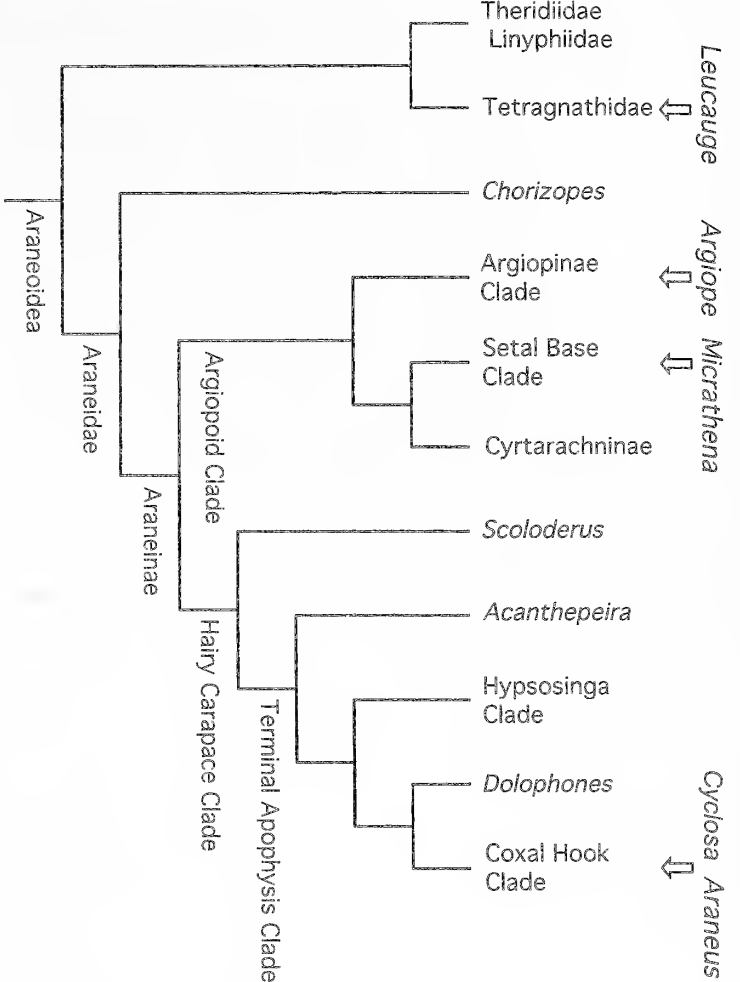


Figure 1.—An overview of araneoid phylogeny (summarized from fig. 82 in Scharff & Coddington 1997), showing the position of the five genera included in the current study.

(Walckenaer 1805) has a mean adult female body mass of 84.3 mg ($n = 21$, $SE = 5.0$). It occupies moist forests, where it constructs orb webs that have very closely spaced capture spirals and an orientation that ranges from nearly horizontal to vertical. *Cyclosa conica* (Pallas 1772) has a mean adult female body mass of 8.9 mg ($n = 23$, $SE = 0.8$), constructs vertical orb webs, and can be found on exposed shrubbery and on vegetation along forest edges. *Araneus marmoreus* Clerck 1757 has a mean adult female body mass of 677.1 mg ($n = 15$, $SE = 75.0$), constructs vertical orb webs on vegetation along forest edges, and uses a signal line to monitor its web from a retreat made of a curled leaf.

Thread collection and storage.—I collected some capture threads directly from orb webs on samplers made from microscope slides with raised, parallel, rectangular supports glued at 4.8 mm intervals to their upper surfaces. Doubled-sided tape atop these supports maintained the thread's native tension. In some cases, a sector of an orb web was first captured on an 18 cm diameter polished

aluminum ring with double-sided tape on its upper rim and thread samples were collected from this ring in the laboratory.

Threads were collected in the morning to ensure that they were fresh. However, it was not possible to determine precisely how old these threads were. Thread droplets were measured 2–4 h thereafter, and their stickiness was measured no more than 3 h later. Threads were maintained and measured at 23–25 °C and 60–62% RH (Table 1). Under these conditions, the hygroscopic properties of viscous threads maintain droplet volume (Townley et al. 1991). However, I did not attempt to measure the stability of droplet dimensions.

The thread properties of each species probably perform optimally under the environmental conditions typical for that species. However, Townley et al. (1991) show that the size of viscous thread droplets can change as they take up the atmospheric water and that this is influenced by ambient humidity. Thus, temperature and humidity differences among habitats probably influence droplet volume and this feature may change over the course of a day. By maintaining threads under stable and fairly uniform temperature and humidity conditions, I believe that this fluctuation was minimized and that I established conditions that were acceptable for the broad comparisons made in this study.

Droplet volume.—I first examined a thread under a dissecting microscope to ensure that it was not damaged. Its droplets were then measured at 500 X under a compound microscope. Both the repeatability and resolution of measurement of droplet diameters were about 0.4 μm (Opell 1997). I determined thread volume from measurements (Fig. 2) of the distance (D) spanned by a series of droplets (N) and the lengths (L, dimension parallel to thread length) and widths (W) of two droplets. Droplet length influenced the number of droplets included in a series as shown in Table 1. Two thread sectors were measured for each spider's web (subscripts 1 and 2). When droplet size was not uniform, I measured representatives of the larger and smaller droplets. Table 1 gives the mean intra-sample range of droplet length and width for each species. Increasing the number of droplets and thread sectors measured increases the accuracy with which thread volume can be computed. All measurements were in μm . I used the follow-

ing formulas to compute the volume (μm^3) of viscous material in the droplets of a 1-mm length of adhesive thread.

Mean Droplet Radius (MDR)

$$= (\text{Grand Mean of L and W})/2. \quad (1)$$

Droplet Volume (DV)

$$= 4 \times \pi \times \text{MDR}^3/3. \quad (2)$$

Droplets per mm (DPMM)

$$= ((N_1 + N_2)/(D_1 + D_2)) \times 1000. \quad (3)$$

Droplet Volume per mm (DVPMM)

$$= \text{DV} \times \text{DPMM}. \quad (4)$$

Interdroplet volume was not included in these calculations, as it is small and does not appear to contribute to glycoprotein granule formation (Opell 1997). Values of droplet volume include the volume of the supporting axial fibers that run through the droplets. I did not attempt to factor out this volume for two reasons. First, for the species studied axial fiber diameters are small, ranging from 1.03–5.37 μm (Opell & Bond 2001); and fibrils comprise only a small part (0.07–0.75%, mean 0.35%) of a droplet's volume. Second, the objective of this study was to devise a simple method for estimating thread stickiness. Axial fiber diameter is difficult and time-consuming to measure (Opell & Bond 2001) and its inclusion is inconsistent with this objective.

Thread stickiness.—Thread stickiness is reported as the force (μN) required to overcome the stickiness of a 1 mm length of thread. As described in more detail by Opell (1997), this was determined by first pressing a 2 mm wide piece of 320 grit, 3M waterproof silicon carbide sandpaper against a thread with a standard force. The force required to pull the contact plate from the thread was then measured with a strain gauge made from a stainless steel needle. The particles on the surface of these sandpaper plates were of uniform size and distribution (Opell 1993) and these plates registered the same stickiness for adhesive threads as did contact plates made from fleshfly wings (Opell 1997). Thus, the stickiness values obtained by this method were similar to those registered by a representative insect surface.

Phylogenetic analyses.—Features of species that are evolutionarily related are not, in

Table 1.—Droplet measurements and thread stickiness values and the conditions under which threads were stored and measured (mean ± 1 standard error). The mean intra-sample range of droplet length and width is given in parentheses.

Family	Temp.	Percent	Mean	Droplet	Droplet	Droplets	Droplet	Thread
Species		relative	droplets	length	width	per	volume	stickiness
(individuals)	(°C)	humidity	per series	(μm)	(μm)	mm	(μm ³ /mm × 10 ³)	(μN/mm)
Tetragnathidae	25 ± 0.1	61 ± 0.5						
<i>Leucauge venusta</i>			8	12.5 ± 0.51	10.1 ± 0.42	41.4 ± 2.1	31.3 ± 2.6	19.3 ± 1.3
(25)				(2.2)	(2.1)			
Araneidae	23 ± 0.3	60 ± 0.5						
<i>Argiope trifasciata</i>			13	43.0 ± 2.1	29.3 ± 1.3	9.4 ± 0.56	257.7 ± 31.4	28.2 ± 1.9
(33)				(21.0)	(18.8)			
<i>Micrathena gracilis</i>	23. ± 0.2	62 ± 0.4	4	24.9 ± 1.0	19.8 ± 0.72	20.2 ± 0.92	117.2 ± 9.3	26.4 ± 1.6
(17)				(5.3)	(6.2)			
<i>Cyclosa conica</i>	24 ± 0.1	61 ± 0.5	6	11.8 ± 0.64	9.6 ± 0.56	34.0 ± 2.4	21.3 ± 2.2	9.6 ± 0.76
(18)				(3.9)	(3.9)			
<i>Araneus marmoreus</i>	23 ± 0.2	61 ± 0.2	9	59.6 ± 3.6	46.9 ± 3.1	6.9 ± 0.80	480.2 ± 55.7	32.0 ± 2.7
(21)				(23.2)	(21.5)			

a strict sense, independent and, therefore, violate the assumptions of parametric statistics (Felsenstein 1985; Harvey & Pagel 1991). Therefore, I employed the independent contrast (IC) method of Felsenstein (1985) to determine if the droplet volume and stickiness of threads produced by adult female spiders were related. This method accounts for the influence of phylogeny on continuous characters by analyzing differences in the values expressed by sister taxa (both extant taxa and their inferred ancestors). These differences are then normalized and relationships among the resulting independent contrast values are analyzed with regression statistics. I used the Comparative Analysis of Independent Contrasts program of Purvis & Rambaut (1995) to compute normally distributed independent contrast values and the S.A.S statistical package (S.A.S. Institute Inc., Cary, North Carolina) to perform this and the other statistical tests reported in this study.

Ontogenetic analyses.—I examined developmental changes in the droplet volume per mm and the thread stickiness per mm of threads produced by *A. trifasciata* and *M. gracilis*. I selected these species because threads produced by adult females have similar stickiness values but differ greatly in the size and distribution of their droplets (Table 1). *Argiope trifasciata* produces threads with much greater droplet volume but only half as many droplets per mm as threads of *M. gracilis*.

I collected threads from the field rather than from spiderlings reared in the laboratory to reduce the possibility that spider diet would unnaturally affect the results of this study. I collected threads from *A. trifasciata* from early June to late October at a site where the previous year I observed a large number of adult females of this species and only one individual of the sympatric species, *A. argentata* Lucas. I collected threads of *M. gracilis* from early June to late August at a site where, for two years, this was the only species of this genus that I observed. As spiderlings do not emerge synchronously from egg sacs and as it was not possible to permanently mark spiderlings, I was unable to determine precisely the age of individuals included in each developmental series. My approach was, therefore, to sample these populations regularly to obtain threads produced by immatures of increasing size and, eventually, by adult spiders, thereby obtaining capture threads from each species that had droplets of increasing size.

RESULTS

Phylogenetic analysis.—Droplet volume ranged from 21–480 x 10³ μm³ per mm length

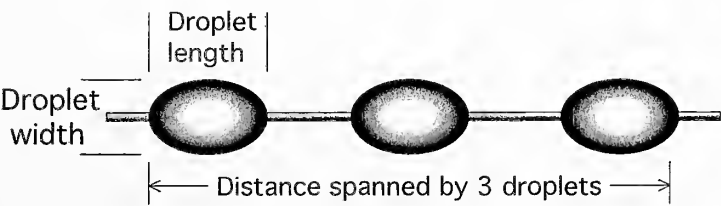


Figure 2.—Measurements used to compute droplet volume.

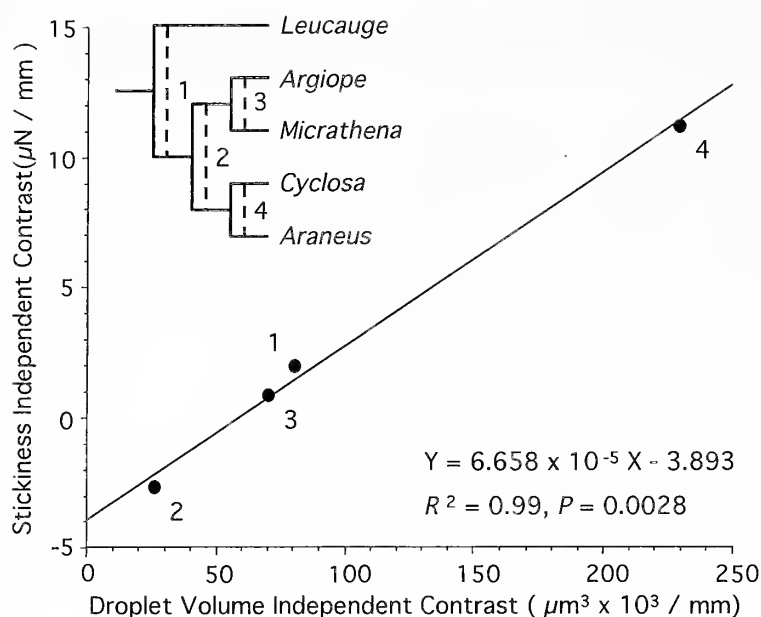


Figure 3.—Relationship between change in droplet volume per mm and thread stickiness, as determined by an independent contrast analysis. Numbers refer to independent contrast values between the sister taxa identified in the pruned phylogeny.

of capture thread and stickiness ranged from 9.6–32.0 μN per mm of thread length (Table 1). IC analysis supports the hypothesized association between droplet volume and thread stickiness by showing that the IC values for droplet volume and thread stickiness are directly related (Fig. 3; $n = 4$, $F = 356.64$, $P = 0.0028$, $R^2 = 0.99$).

Ontogenetic analysis.—For threads of both *A. trifasciata* and *M. gracilis* with droplets of increasing size, droplet volume per mm was directly related to thread stickiness per mm (Fig. 4; $n = 94$, $F = 33.25$, $P = 0.0001$, $R^2 = 0.27$ and $n = 67$, $F = 69.25$, $P = 0.0001$, $R^2 = 0.52$, respectively). When \log_n droplet volume per mm was used, a better fit for *A. trifasciata* was obtained and the fit for *M. gracilis* did not change appreciably ($F = 83.44$, $P = 0.0001$, $R^2 = 0.48$ and $F = 67.90$, $P = 0.0001$, $R^2 = 0.51$, respectively). An analysis of covariance test showed that slopes of the regression lines for \log_n droplet volume per mm and thread stickiness did not differ ($F = 0.20$, $P = 0.65$) and a comparison of the intercepts of the two species regression lines showed that they also did not differ ($F = 1.41$, $P = 0.24$). Thus, a single regression line satisfactorily describes developmental changes in \log_n droplet volume per mm and the stickiness of these two species' capture threads (Fig. 4).

Characteristics of threads produced by adult females.—The IC analysis documented that there is a direct relationship between

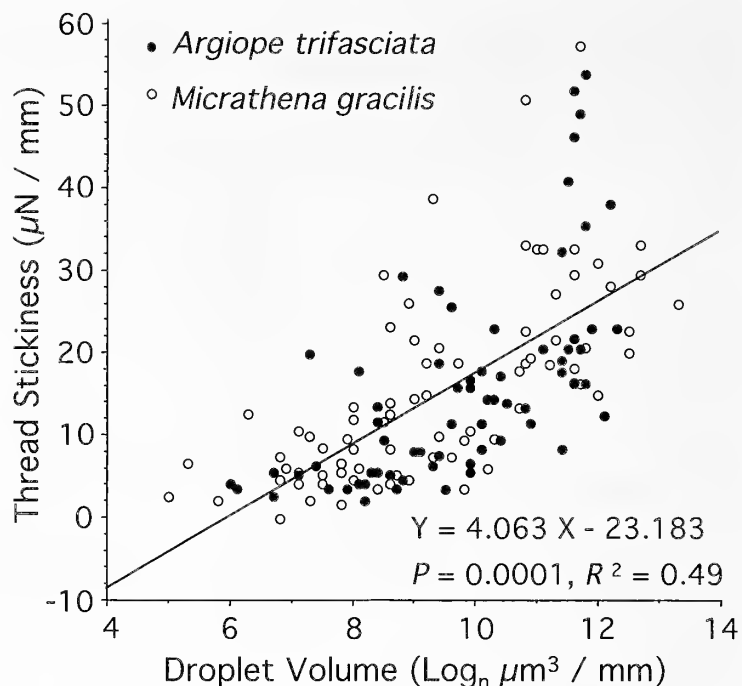


Figure 4.—Developmental changes in droplet volume and thread stickiness of *Argiope trifasciata* and *Micrathena gracilis*. A common regression line is shown, as the slopes and intercepts of the two species' regression lines do not differ.

droplet volume and thread stickiness (Fig. 3). However, as IC values are derived values, they do not depict the actual relationship between these features. Therefore, I employed traditional regression analysis to describe the relationship between droplet volume per mm of thread length and thread stickiness. In one analysis I used the pooled values of adult females from the five species (Fig. 5; $n = 113$, $F = 58.26$, $P = 0.0001$, $R^2 = 0.34$) and in another the mean values of each of the five

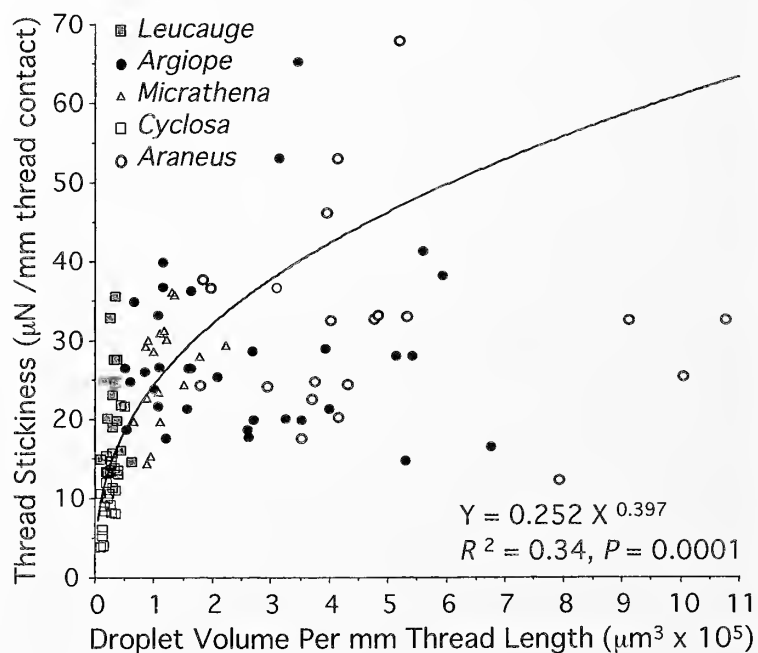


Figure 5.—Relationship between droplet volume per mm of thread and thread stickiness for adults of five araneoid species.

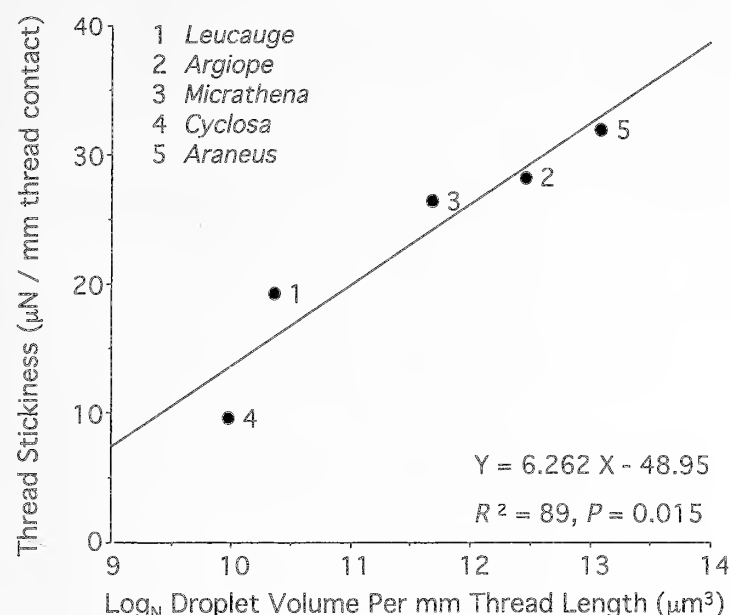


Figure 6.—Relationship between the mean adult values of droplet volume per mm of thread and thread stickiness for five araneoid species.

species (Fig. 6; $n = 5$, $F = 25.03$, $P = 0.015$, $R^2 = 0.89$). In both analyses droplet volume was directly related to thread stickiness and in both this relationship was curvilinear. That is, stickiness increased at a slower rate than did droplet volume. Consequently this relationship was best explained by formulas that used log values of droplet volume (Figs. 5, 6). The plot of all values (Fig. 5) shows that as a thread's droplet volume increases, so too does the variance of its measured stickiness.

Only for the threads produced by adult female *C. conica* was there a direct relationship between droplet volume per mm thread length and thread stickiness ($n = 18$, $F = 11.71$, $P = 0.0041$, $R^2 = 0.41$, stickiness ($\mu\text{N}/\text{mm}$) = 0.00022 thread volume ($\mu\text{m}^3/\text{mm}$) + 4.860). In the other four species this relationship was not significant ($0.13 < P < 0.94$). When \log_n droplet volume per mm thread length was used, the relationship for *C. conica* remained significant ($n = 18$, $F = 12.29$, $P = 0.0029$, $R^2 = 0.43$, stickiness ($\mu\text{N}/\text{mm}$) = $4.370 \log_n$ thread volume ($\mu\text{m}^3/\text{mm}$) - 33.53) and for the other four species it was insignificant ($0.08 < P < 0.84$).

Modeling thread stickiness.—I developed and evaluated three models to predict the stickiness of adhesive threads (Fig. 7): one based on adult thread features, one based on ontogenetic data, and one based on a trial-and-error empirical examination of droplet values. Because phylogenetic analyses demonstrate a direct relationship between droplet volume per mm and thread stickiness, I based the first

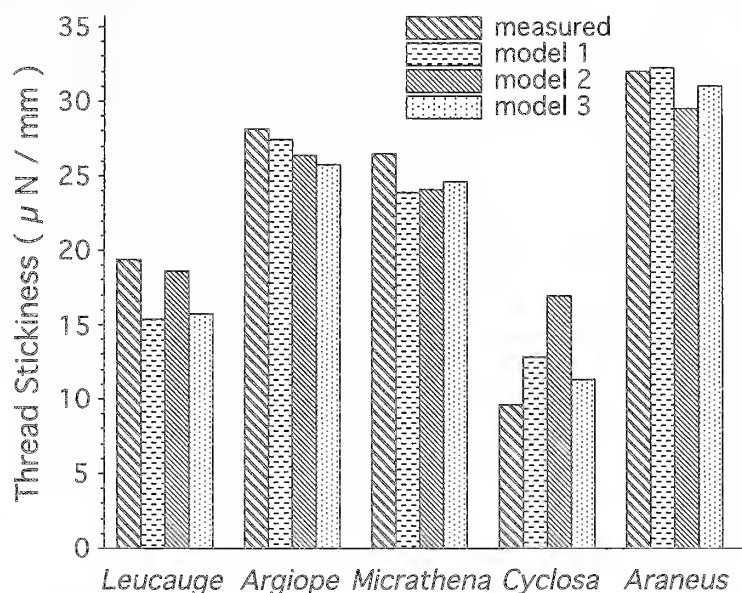


Figure 7.—Comparison of measured stickiness (S) and the values predicted by three models. Model 1 is based on the regression of mean adult values and has the formula: $S = \log_n$ droplet volume per mm $\times 6.262 - 48.95$. Model 2 is based on the ontogenetic regression and has the formula: $S = \log_n$ droplet volume per mm $\times 4.063 - 23.183$. Model 3 is an empirical model and has the formula: $S = \log_n$ (droplet width \times droplet length \times droplets per mm) $\times 13.184 - 96.288$.

model on a regression of the mean adult values of these variables (Fig. 6). The second model uses the common ontogenetic regression formula shown in Fig. 4 to predict stickiness. The third model is based on the observation that the product of droplet length (DL), droplet width (DW), and the number of droplets per mm (DPMM) successfully predicted thread stickiness ($F = 40.24$, $P = 0.008$, $R^2 = 0.93$) according to the following formula:

Thread Stickiness

$$= \log_n(\text{DL} \times \text{DW} \times \text{DPMM}) \times 13.184 - 96.288. \quad (5)$$

Figure 7 compares the performance of these three models. For model 1 the mean absolute difference between each of the five species' measured and predicted stickiness values was 13.23%, for model 2 it was 20.52%, and for model 3 it was 10.76%.

DISCUSSION

Phylogenetic and ontogenetic analyses support the hypothesis that the volume of material in an adhesive thread's droplets is directly related to its stickiness. Models based on these comparisons provide good estimates of the

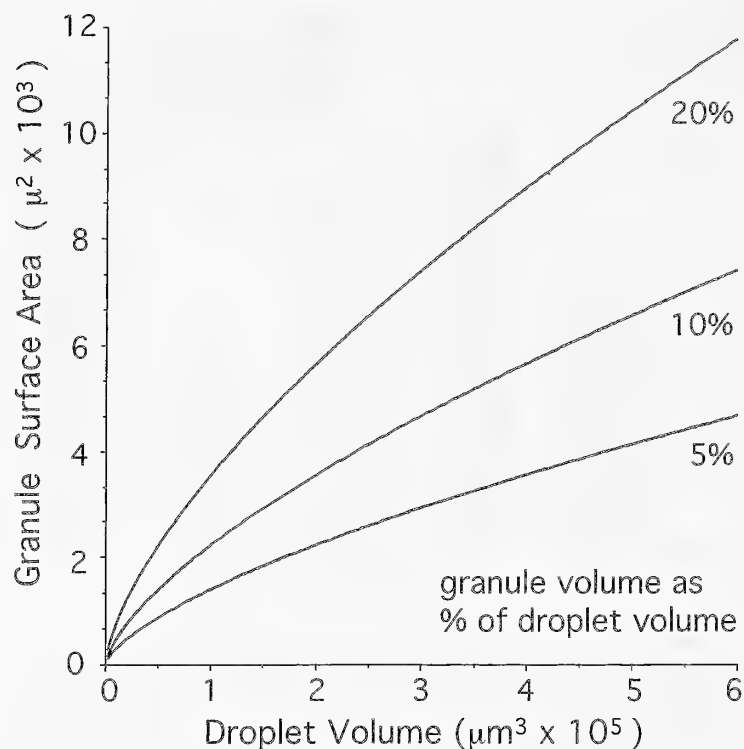


Figure 8.—Relationship between the volume of a viscous droplet and the surface areas of its glycoprotein granule, with granule volume being computed as 5%, 10%, and 20% of droplet volume.

stickiness of adhesive threads that have a wide range of droplet size and distribution patterns and that are produced by spiders of greatly different masses. The simplicity and accessibility of this approach will facilitate the inclusion of thread stickiness in studies that examine the properties and performance of spider orb webs. However, it is important to remember that these models are based on the threads of only five species from the temperate region of North America that belong to two families and that they represent only a small part of araneoid diversity. Additionally, variance in the stickiness predicted by the droplet volume of threads (Fig. 5), particularly the threads of large araneoids, such as *A. trifasciata* and *A. marmoreus*, requires that the capture threads of many individuals be measured to usefully estimate the stickiness of a species' threads.

The curvilinear relationship between droplet volume per mm of thread length and thread stickiness (Figs. 4, 5) is most easily explained by the relationship between the volume of a viscous droplet and the surface area of the glycoprotein granule that lies within it. If contact between a thread's granules and an object is responsible for thread stickiness, then the surface areas of granules should be directly related to thread stickiness. The model presented in Fig. 8 shows that as granule size

increases relative to droplet volume, granule area and, presumably, thread stickiness increases. However, this model also shows that when granule volume is a constant percent of a droplet, granule surface area increases more slowly than does droplet volume. Thus, it appears that the benefits (in terms increased thread stickiness) of producing capture threads with larger adhesive droplets diminish unless there is also an increase in granule volume relative to droplet volume. Similarities in the shapes of the curves in Figs. 5 & 8 suggest that no such compensatory increase in granule volume has occurred in the species that were studied. However, the similarity of these curves may be coincidental and the shape of the curve in Fig. 5 may instead reflect interspecific differences in the composition and concentration of glycoproteins and hydroscopic compounds in the droplets of these species.

The ability of an orb web to intercept prey is related to its capture area (the area between the inner- and outer-most capture spiral of the web), whereas the web's ability to retain prey is related to its stickiness per capture area (Opell 1999b). The origin of modern adhesive orb webs like those treated in this study was associated with an increase in the stickiness per capture area (Opell 1999b). However, there were differences in the stickiness per capture area among the five adhesive orb webs examined by Opell (1999b). The methods described in this study make it easier to examine the consequences of these differences in web design. For example, do larger spiders tend to construct webs characterized by a greater capture area and a smaller stickiness per capture area because they are better equipped to subdue larger prey than are smaller spiders? Are the running and response speeds of a spider associated with the capture area and stickiness per area of its orb web? Are horizontal orb webs characterized by a greater capture areas and smaller stickiness per capture area because they tend to capture smaller, more erratically flying insects (Craig 1987)? Does the stickiness per capture area of an orb web influence the guild of insects that it captures? These and other questions can be addressed by estimating and considering capture thread stickiness.

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**A COMPARATIVE STUDY OF PHENOLOGY AND DAILY
ACTIVITY PATTERNS IN THE WOLF SPIDERS *PARDOSA*
MILVINA AND *HOGNA HELLUO* IN SOYBEAN
AGROECOSYSTEMS IN SOUTHWESTERN OHIO
(ARANEAE, LYCOSIDAE)**

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ABSTRACT. We studied the phenology and the daily activity patterns of *Pardosa milvina* Hentz 1844 and *Hogna helluo* (Walckenaer 1837) in replicated soybean fields in southwest Ohio over three years (1994–1996) using pitfall traps. For the phenology study we established an array of five pitfall traps in 12 replicate 0.42 ha fields. These traps were either set for two days at two-week intervals (1994), or for three days at three-week intervals (1995 & 1996), over the field season from May–October on a total of 20 trap dates. We found that *P. milvina* was more common overall, and found evidence for one population peak per year. Numbers of *H. helluo* tended to be lowest in the earlier censuses, and we found evidence for one peak of male activity per year. The immature male and female, and adult female *H. helluo* were larger (based on carapace width) than the immature male and female, and adult female *P. milvina* on most trapping dates. For the circadian activity periodicity study we used two different drift-fence trap designs, both with dry-cup pitfall traps set for two or three days and checked at 12 h intervals. For three sampling periods in 1994 we found *H. helluo* to be more frequently trapped at night, and for two sampling periods *P. milvina* was more frequently trapped during the daylight hours.

Keywords: Agroecosystem, *Pardosa*, *Hogna*, phenology, soybean, circadian

Spiders are common components of agricultural ecosystems wherever found (Luczak 1979; Young & Edwards 1990). Because spiders often attain high population densities in crop systems, there exists the potential for pest insect population suppression (Riechert 1999; Sunderland 1999). For this reason, there has long been interest in the population dynamics of spiders in agricultural ecosystems (Whitcomb 1967; Breene et al. 1993; Draney 1997; Greenstone & Sunderland 1999), and the ways in which crop management practices impact spider abundance and diversity (Bishop & Riechert 1990; Balfour & Rypstra 1998; Rypstra et al. 1999). Despite this interest, there have been relatively few studies which focus on the biology of specific spider taxa.

Wolf spiders (Araneae, Lycosidae) are one

of the most abundant components of the spider community in agroecosystems (LeSar & Unzicker 1978; Luczak 1979; Young & Edwards 1990; Bishop & Riechert 1990). One wolf spider genus in particular, *Pardosa* C.L. Koch 1847, is a relatively well-studied inhabitant of agroecosystems across the northern hemisphere (e.g., Nyffeler & Benz 1988; Nyffeler & Breene 1990; Marshall & Rypstra 1999 a, b; Kiss & Samu 2000; Samu et al. 1998). The relatively large body of research on *Pardosa* is probably a result of its relatively high abundance in agricultural fields. The reasons for *Pardosa*'s conspicuous success in the structurally-simple and seasonally-barren habitats provided by crop fields may lie in an evolved adaptation to life in riparian corridors and other periodically flooded habitats, which would pre-adapt them to the annual cycle of disturbance found in most row-crop systems (Luczak 1979; Wissinger 1997; Marshall & Rypstra 1999 a, b).

We have found *P. milvina* Hentz 1844 to be the most common vagrant spider in the

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fields in which we work, and have observed densities of over 100/m² (Marshall & Rypstra unpublished data). We have also found the ecologically-divergent *Hogna helluo* (Walckenaer 1837) in these fields, but at much lower densities. We have found that these two spider species use the same microhabitats in similar ways (Marshall & Rypstra 1999 b), yet their behavior (Walker et al. 1999 a, b) and ecology (Marshall et al. 2000) make for a revealing contrast. *Pardosa milvina* is much more vagile than *H. helluo* (Walker et al. 1999 a), is more of a habitat generalist (Marshall & Rypstra 1999 a, b), and lives in the agricultural fields year-round (Marshall & Rypstra 1999 b). In addition, *P. milvina* exhibits complex anti-predator behaviors when exposed to *H. helluo*-associated cues (Persons et al. 2001), which suggests a shared evolutionary history.

In this paper we report on the population dynamics of *P. milvina* and *H. helluo* in an array of 12 replicate soybean fields as revealed by a study of pitfall trap samples. We conducted our studies in fields managed for research into the impact of tillage regime on the spider community structure of the fields. We present data on the impact of tillage regime on spider numbers elsewhere (Marshall & Rypstra 1999 b).

METHODS

Field site.—The soybean plots used in this study are located at the Ecology Research Center of Miami University in Butler County, Ohio, USA. The data were conducted within 12, 0.42 ha soybean monoculture plots. The plots are in a 2 by 6 rectangular array oriented in a north-south direction. Each plot measures 60 x 70 m with a 15 m mowed grassy strip border separating them from one another and the surrounding habitats (Kemp & Barrett 1989). Six of the plots were planted and maintained using conventional tillage practices, and the other six were managed using conservation tillage practices (see Marshall et al. 2000 for details). In 1994 this tillage regime was combined with a “no-herbicide treatment” in half of the plots for a total of four treatments. This elaboration was dropped in subsequent years (1995 & 1996). Tillage treatments were assigned randomly the first year and maintained between years in the same plots. The conventional tillage plots were

tilled in early May. Soybeans were planted in late May. Pre-emergence herbicides were applied immediately after planting. In early June post-emergence herbicide was applied to the conservation tillage plots to control ragweed. The conventional tillage plots were again cultivated in July. No insecticides were applied to any plot at any time.

Phenology.—We used a pitfall trap that includes an elevated wooden cover to exclude rain and vertebrates (Cady & Sugg 1998). We placed five traps in each of 12 replicate plots. In each plot there was one trap in each corner, placed approximately 10 m from each side, and one trap in the center of the plot. Each trap contained several cm of a 50/50 ethylene glycol/water solution.

In 1994 the traps were set at two week intervals for 9 two-day trapping periods. In 1995 and 1996 we ran the traps at three week intervals for 5 and 6 three-day trapping periods respectively. We counted and measured the size of all the *H. helluo* and *P. milvina* under a dissecting microscope to the nearest 0.1 mm using an ocular micrometer. We used carapace width as an estimator of spider body size (Hagstrum 1971; Marshall & Gittleman 1994).

In our fields we also have a small number of *P. saxatilis* Hentz 1844 and *H. aspersa* (Hentz 1844). These two taxa may be confused with *P. milvina* and *H. helluo*, respectively, when immature. Because these two congeners were rare in the soybean agroecosystem (< 1%, based on abundances of the easily-identified adults) we categorize all immature *Pardosa* as *P. milvina* and all immature *Hogna* as *H. helluo*.

Daily activity periodicity.—We used drift fence traps in 1994 to test for differences in activity periods in *H. helluo* and *P. milvina*. The traps were constructed of 25 cm wide sheets of metal 3.05 m long. At 0.75 m intervals along each side of the fence 250 ml plastic cups were buried flush with the ground surface against the fence. Between 2–6 August we set up two drift fences approximately 18 m long. We placed one in a conservation tillage plot and the other in a conventional tillage plot. During the August trapping period each drift fence trap had a total of 48 cups (24 on each side). Between 6–9 September and 3–6 October we ran six smaller trap arrays in six plots, three in conventional tillage plots and

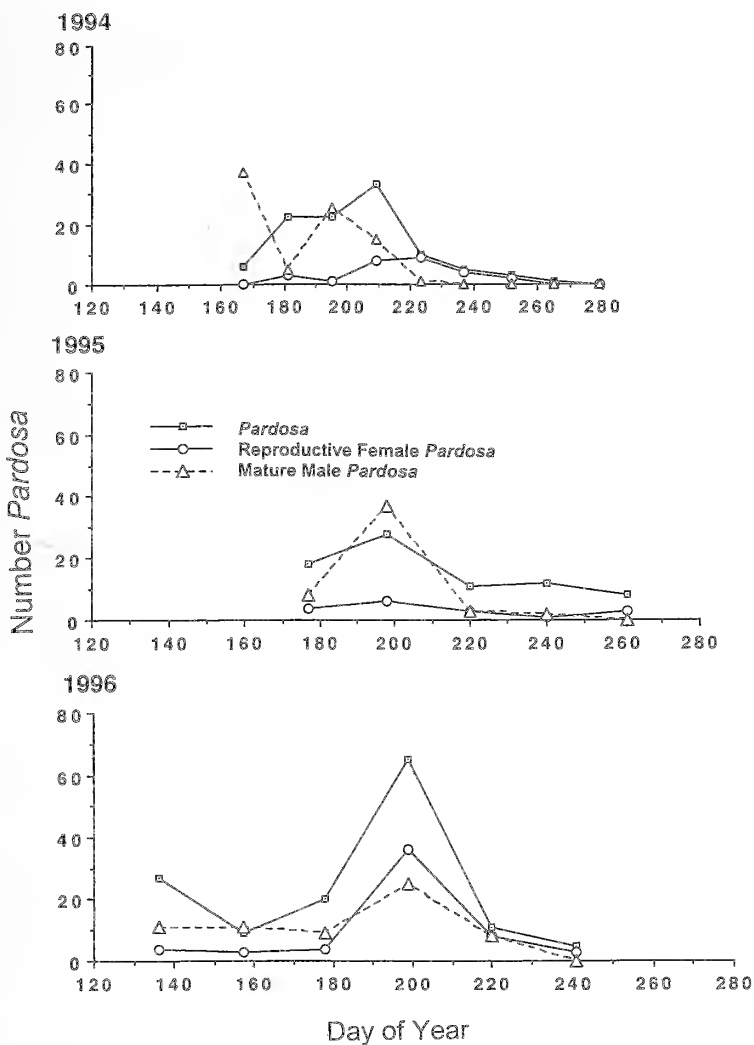


Figure 1.—Total *Pardosa milvina* collected in 60 pitfall traps set in 12, 0.4 ha soybean fields (five per field) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. “*Pardosa*” refers to immature and non-reproductive adult female *P. milvina*, “Reproductive Female *Pardosa*” refers to adult female *P. milvina* carrying eggs or spiderlings, and “Mature Male *Pardosa*” refers to sexually mature male *P. milvina*.

three in conservation tillage plots. Each trap array was approximately 9 m long and each had a total of 24 cups, 12 to a side. At all dates each drift fence trap array was oriented row-wise (east-west) at an arbitrarily selected spot in the plot. Traps were set in the evening on the first day (ca. 2000 h) and all cups checked at 12 h intervals thereafter. Each time the trap was checked any *H. helluo* and *P. milvina* captured were counted and released on the opposite side of the trap from which they were captured. In August we checked the traps four times for two sampling days, in September and October we checked the traps 6 times for three sampling days. We analyzed the data using a binomial test for an expected proportion of 0.5 trapped during the day versus night sampling period for each species to test the null hypothesis of no difference be-

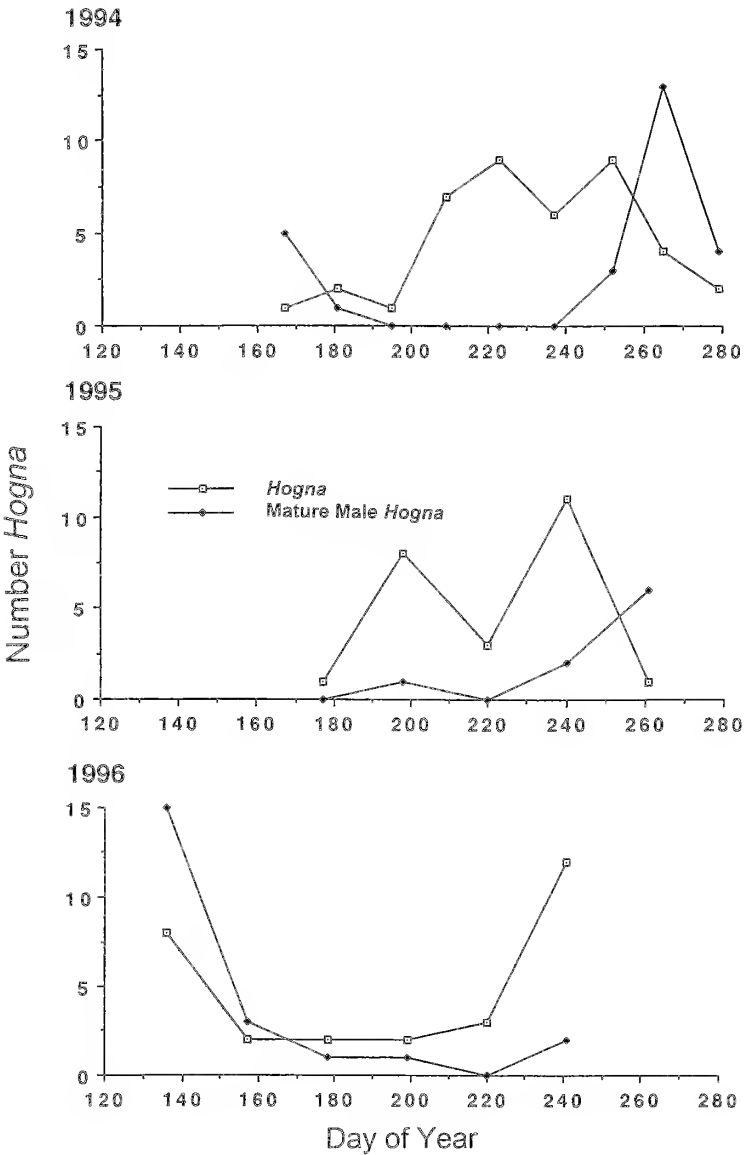


Figure 2.—Total *Hogna helluo* collected in 60 pitfall traps set in 12, 0.4 ha soybean fields (five per field) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. “*Hogna*” refers to all immature and adult female *H. helluo* and “Mature Male *Hogna*” refers to adult male *H. helluo*.

tween the total numbers trapped during the day versus night. All spider collections made during this research are in the collections in the Hefner Museum of the Department of Zoology, Miami University.

RESULTS

Phenology.—We found that *P. milvina* was overall more common than *H. helluo* (Figs. 1, 2). *Pardosa milvina* exhibited a consistent population peak around Julian date 200 (in mid June). Captures of both immature and adult *P. milvina* peaked around this date in all three years, as did the numbers of female *P. milvina* carrying eggs or spiderlings.

The population trends for *H. helluo* are less clear. In general there were greater numbers trapped both early and late in the year than during mid-season. We were unable to assess

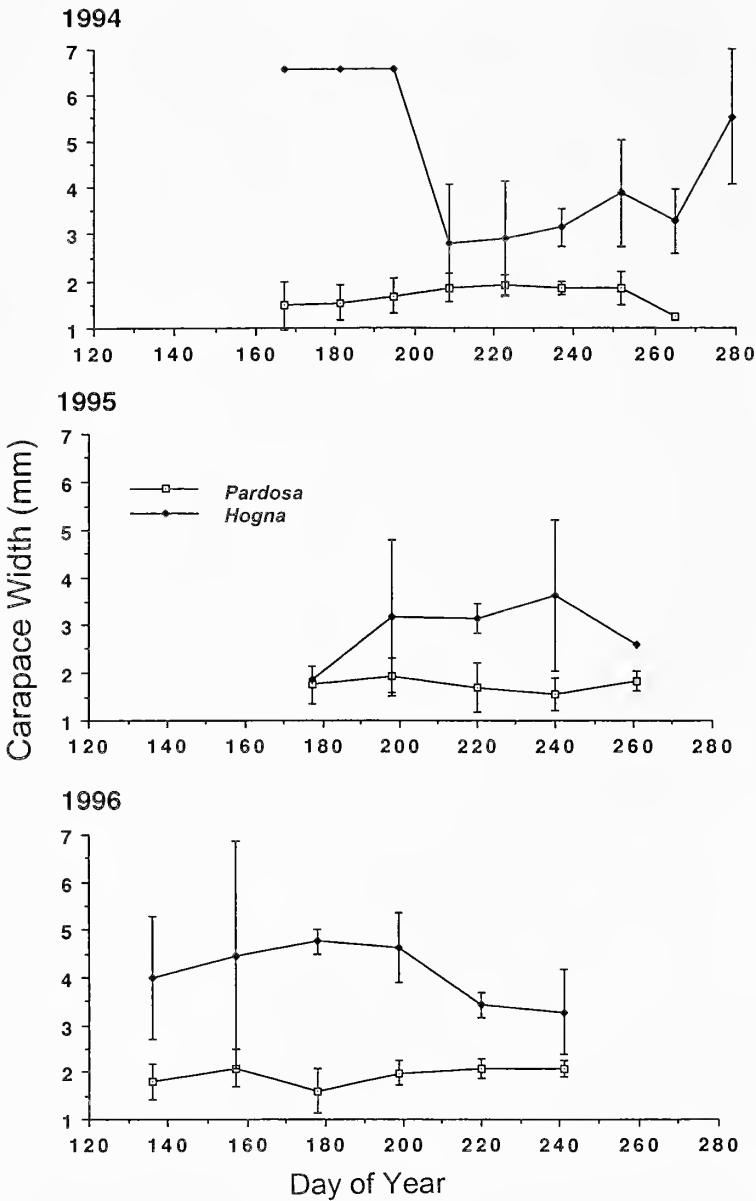


Figure 3.—Comparison of carapace widths for all immature and adult female, and all immature male *Hogna helluo* and *Pardosa milvina* collected at each date in 12, 0.4 ha soybean fields at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Expressed as means \pm 1 SD.

female reproduction since adult female *H. helluo* with egg sacs or spiderlings were rarely found because they take refuge in burrows when reproductive (Dondale & Redner 1990; Walker et al. 1999 b). There seemed to be a uniform increase in the numbers of adult males in the fall and spring. This indicates that males may mature at the end of the summer and over winter as adults, or over winter as subadults that mature in the spring. The unimodal timing of sexually mature males indicates that *H. helluo* may be seasonal in its breeding.

We were able to compare mean body size of the trapped populations of the immature stages of both sexes and adult females between *H. helluo* and *P. milvina* (Fig. 3). We arbitrarily selected a minimum of three of the

Table 1.—Comparison of body sizes for immature male and female and adult female *Pardosa milvina* versus *Hogna helluo* (as estimated by carapace width) trapped using 60 pitfall traps, five in each of 12 soybean fields at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Data presented are for trapping dates at which at least 3 specimens *H. helluo* (the rarer species) were captured. Based on a Bonferroni-adjusted alpha level of $P = 0.005$, only the P values marked with an asterisk indicate significant differences in size between the species populations.

Year	Day	<i>T</i>	Df	<i>P</i>
1994	209	−4.05	38	0.0002*
1994	223	−2.74	17	0.1390
1994	237	−6.75	9	0.0001*
1994	252	−2.97	10	0.0140
1995	198	−3.73	34	0.0007*
1995	220	−4.478	12	0.0008*
1995	240	−4.42	21	0.0002*
1996	136	−8.03	33	0.0001*
1996	220	−8.75	10	0.0001*
1996	241	−2.921	15	0.0105

rarer species on a given trap date as a cut-off for inclusion in a statistical comparison of carapace widths. Using these criteria, we were able to make a comparison on 10 out of the total of 20 trapping dates over the three years (Table 1). Because we were performing replicate statistical tests (10) and because our selected alpha level of $P = 0.05$ means that 1 in 20 tests could indicate significant differences based on chance alone, we used a simultaneous Bonferroni adjustment procedure. This entailed dividing the selected alpha level by the number of tests performed. Thus, our adjusted alpha level was now $P = 0.005$. Using these criteria, we found that the *H. helluo* we trapped were significantly larger than the *P. milvina* on 7 of the 10 dates for which this test was performed.

Daily activity periodicity.—There was an obvious trend for *H. helluo* to be more active at night, and *P. milvina* during the day. There were a total of 98 *H. helluo* and 138 *P. milvina* captures over the three sampling dates. Some of these were likely to be recaptures, but during pilot studies when we marked *P. milvina*, we had recapture rates approximating 5%. No *P. milvina* were captured during the October trapping period. For the three dates for *H. helluo* there was a significant deviation

Table 2.—Results of binomial test on frequency of capture using drift-fence live pitfall traps in either two soybean fields, 48 cups each (2, 4, & 6 August 1994) or six soybean fields, 24 cups each (7–9 September and 4–6 October 1994) at the Miami University Ecology Research Center, Oxford, Butler Co., Ohio. Data reported are total captures during the day (0800 h–2000 h) versus night (2000 h–0800 h) for *Hogna helluo* and *Pardosa milvina* for the three sampling periods.

Date	Taxon	Number		P
		Total number trapped	trapped during the day	
August	<i>H. helluo</i>	27	5	0.0006
	<i>P. milvina</i>	124	90	0.0
September	<i>H. helluo</i>	39	2	0.0
	<i>P. milvina</i>	12	9	0.054
October	<i>H. helluo</i>	30	6	0.00055
	<i>P. milvina</i>	NC*	NC	

* None captured.

from random activity for day versus night (Table 2). For *P. milvina* there was only a significant deviation for one of the two dates for which there were data (Table 2).

DISCUSSION

Pardosa milvina and *H. helluo* were both common elements of the spider fauna of the soybean fields under study. All life stages of both species are found in the fields throughout the summer growing season. *Pardosa milvina* overwinters in the fields as subadults, and can even be observed active in the fields in mid-winter on warm days (December–February; S. Marshall, pers. obs.). The circannual pattern for *H. helluo* is less clear, other than the higher numbers of adult males trapped at the beginning and end of the field season. It may be that *H. helluo* mate in the fall or early spring, with females producing successive egg sacs during the summer. The comparison of body sizes of the adult female and subadult female and male population did not reveal any strong pattern. We had hoped to see evidence of growth of the spiders through the year as increased mean body size for the trapped population. We are left to guess about the number of generations of *H. helluo*. Based on data from laboratory rearing studies (R. Balfour unpublished data) we tentatively conclude that *H. helluo* has at least a two year life cycle.

There have been several studies of the phenology of *P. milvina*. Whitcomb (1967) reported that it matured in an average of 96.8 days and was univoltine. While Whitcomb did note that *P. milvina* could theoretically pass two generations a year in the Arkansas agroecosystems where he worked, he concluded that there was no proof of this from the field. Both Kaston (1981) and Dondale & Redner (1990) report that *P. milvina* is univoltine and overwinters in the immature stages in the northern USA. Wolff (1981) studied the distribution and phenology of several *Pardosa* species of Michigan and found that *P. milvina* was univoltine and was reproductive at approximately the same dates as the *P. milvina* in southwest Ohio. Draney (1997) found that *P. milvina* had a single pronounced peak of numbers of adult males in March at his north Georgia field site. There have been other studies of the phenology of other *Pardosa* species. Yeargan (1975) studied *P. ramulosa* (McCook 1894) in California alfalfa fields and found that the spiders were most abundant in August and September. Samu et al. (1998) studied *P. agrestis* Westring 1861 in an agricultural landscape in Hungary. Using a combination of suction sampling and pitfall traps they found evidence for two peaks in abundance during the summer. They also observed that *P. agrestis* overwintered as subadults. They generated two hypotheses to explain the pattern: 1. There are two generations a year, and 2. the two peaks represented the maturation of early and late season cohorts of spiderlings. Buddle (2000) studied the phenology of *P. moesta* Banks 1892 and *P. mackenziana* Keyserling 1877 in a deciduous forest ecosystem in Alberta, Canada. He also found that *Pardosa* overwinters as a subadult, and found a single peak in the abundance of juveniles. Based on field enclosure studies he proposed that these two *Pardosa* species may take two years to mature.

In addition to the pitfall trap returns we report on here, we also have direct-observation hand-census data for the same fields. Using hand census techniques we found evidence for two population peaks in the field. The second peak occurred around the 270th day of the year, in late August (Marshall & Rypstra 1999 b). This was after we had closed the pitfall traps for the season in the present study. We did not record adult males in our hand cen-

suses, nor did we record the size of the spiders trapped. The time intervals between the observed population peaks were approximately 65 d (1995), 70 d (1996) and 90 d (1996). Would this be long enough for a *P. milvina* spiderling to mature and produce young of its own? The only data we have for time to maturation for *P. milvina* are from Whitcomb's 1967 study, which reported a maturation time of 86.1 d for males ($n = 8$) and 107.5 d for females ($n = 9$). It is always hard to interpret laboratory data on time to maturation in spiders because factors such as temperature and feeding regime can have a tremendous impact on the duration of each instar. However, the times Whitcomb reports are long enough to suggest that the length of time between population peaks we observed in the previous study (Marshall & Rypstra 1999 b) are not the result of an over-wintering cohort of immature spiders giving rise to a summer cohort which in turn produced the over-wintering cohort for the following year.

In contrast to the relatively well-studied *Pardosa*, the phenologies of *Hogna* (formerly *Lycosa*) species wolf spiders have not been studied in agroecosystems. Nappi (1965) studied the mating behavior of *H. helluo* in natural habitats in Connecticut. He reports on his observations of the frequency of adult males and females over three years (1961–1963). His data show a peak in numbers for both sexes in mid-summer (approximately late June–early July). This unimodal peak at mid-summer is the opposite of what our traps revealed for the adult males. On the other hand, Kaston (1981) remarking on *H. helluo* in natural ecosystems in Connecticut, noted that females may be found throughout the year, and males in the summer months. Kaston believed that *H. helluo* mates in the spring. He also inferred that the females overwinter as adults and males as immatures. This is not in agreement with our data, where mature males seem to be more prevalent in the late and early season. An alternative hypothesis is that the males are merely more active at this time, which could also account for their prevalence in the pitfall trap samples.

For our 12 h trapping interval studies we found clear evidence that *P. milvina* is most active during the day, and *H. helluo* at night. We have observed both species to be on the soil surface or in the vegetation throughout

the day and night, but each species is evidently most mobile at different times of the day. Other researchers have also noted that *Pardosa* species are conspicuously active during daylight hours. Dondale (1977) found that the *P. saxatilis* in an Ontario meadow were most active between 1100 and 1600 h. Yeargan (1975) found that the *P. ramulosa* he studied in alfalfa fields were most active between 0700 and 1700 hours. In contrast, workers in the southern US have noted nocturnal foraging activity by *P. milvina*. Whitcomb et al. (1963) noted that they observed spiderlings active on cotton plants at night in Arkansas. Hayes & Lockley (1990) observed *P. milvina* with prey during nocturnal surveys of the wolf spider fauna of cotton fields in Mississippi. We have also noted nocturnally active *P. milvina*, observing large numbers of spiders sitting on the upper surface of the leaves of the soybean plants nocturnally during warmer weather (overnight temperatures $> 22^{\circ}\text{C}$).

Both *H. helluo* and *P. milvina* are successful colonists of soybean agroecosystems, despite the fact that they exhibit such divergent ecological strategies. Of the two spiders, only *P. milvina* might be viewed as a true "agrobiont" (Luczak 1979), or a species that resides in the fields year-round. *Hogna helluo* may need to recolonize the fields each spring after the cropping manipulations are over and the crop plants start to develop (Marshall & Rypstra 1999 b).

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MATING SUCCESS AND ALTERNATIVE REPRODUCTIVE STRATEGIES OF THE DIMORPHIC JUMPING SPIDER, *MAEVIA INCLEMENS* (ARANEAE, SALTICIDAE)

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ABSTRACT. The two male morphs of the dimorphic jumping spider, *Maevia inclemens*, differ dramatically in morphology and courtship behavior. The purpose of this study was to examine and compare the mating success of the two male types. Mating success was measured by the number and duration of copulation events, the latency of visual orientation by the female to a courting male, signals of female receptivity, risk of predation by the female, and the number of offspring produced by each morph. The morphs did not differ significantly with respect to copulation success, mating events, mating duration, signals of receptivity or the number of offspring produced. However, males did differ with respect to latency of visual orientation as a function of distance from the female. Near to the female, the gray males attracted female attention in significantly less time than tufted males. Conversely, at far distances from the female, the tufted males attracted female attention in less courtship time. This study suggests that males attain equal levels of mating success and that the two male morphs may have evolved alternative reproductive strategies for courtship at different distances from the female.

Keywords: Mating success, alternative reproductive strategies, jumping spider, dimorphism

Differences within a species for morphological and/or behavioral traits are relatively common in the animal kingdom. These polymorphic forms may evolve as a consequence of opposing selection pressures, producing differences in body size, coloration, physiology and behavior (Greene 1989; Futuyma 1986). Among the rarest forms of polymorphism is male dimorphism, the existence of two distinct male phenotypes within a single species, which has been documented in only a few animal groups (Wilson 1971; Gadgil 1972; Jenni 1974; Gadgil & Taylor 1975; Trivers 1976; Howard 1978; Endler 1980; Krebs & Davies 1987; Clark and Uetz 1992, 1993; Heinemann and Uhl 2000). Many studies suggest that dimorphic male phenotypes evolve via sexual selection through female choice, resulting in males with a particular phenotype being preferentially selected as mates (Darwin 1871; Fisher 1930; Gadgil 1972; Andersson 1982; Andersson 1994). Typically this leads to alternative reproductive strategies (Rubenstein 1980; Dunbar 1982; Arak 1984; Lott 1991) which are often attributed to phe-

notypic differences among males or their differential ability to compete for females (e.g., Reeves 1907; Le Boeuf 1974). However, in addition to sexual selection, distinct male phenotypes may evolve as alternative behavioral strategies (Howard 1978; Krebs & Davies 1987; Christenson 1984), or in response to environmental conditions that favor the use of one mating tactic over another (Reynolds et al. 1993; Moodie 1972). More rarely, genetic differences that predispose males to use a particular tactic (e.g., Lank et al. 1995) have also been reported.

There is considerable evidence that the courtship displays of males affect the mating decisions of females (see review by Andersson 1994) and variation among males typically leads to selection for males with the most desirable traits. Studies in which variation among males is discrete and the influence of interactions among individuals of the same sex is naturally absent can be especially useful for elucidating the evolution of divergent forms (Vinnedge & Verrell 1998). Hence, the presence of male dimorphism within a species

provides a unique opportunity to assess the potential for different levels of mating success associated with alternative reproductive tactics.

To date there have been few investigations of male dimorphism and this is especially true for spiders. The most recent studies include Heinemann & Uhl (2000) reporting on male dimorphism in the linyphid spider *Oedothorax gibbosus* (Blackwall 1841) and Clark & Uetz (1992, 1993) and Clark (1994) on the dimorphic jumping spider, *Maevia inclemens* Walckenaer 1837 (also known under the name *M. vittata* (Hentz) Barrows 1918), a species exhibiting both morphological and behavioral dimorphism (Peckham & Peckham 1889, 1890; Painter 1913, 1914; Barnes 1955; Emerton 1961; Jackson 1982; Clark 1994). Given the advanced visual system of jumping spiders and its importance in reproductive behavior (Forster 1982; Jackson 1982), *M. inclemens* provides an excellent model system for investigating the mechanisms controlling male dimorphism, such as sexual selection through female choice or alternative male mating strategies (Gadgil 1972; Austad 1984).

The dimorphic jumping spider, *Maevia inclemens*, is found in the eastern and midwestern U.S.A. The "tufted" morph is entirely black in body coloration, has black pedipalps, white legs and three tufts of setae located on its anterior cephalothorax. In contrast, the "gray" morph is black and white striped in body coloration with a prominent white stripe above the anterior eyes, it has striped legs, bright orange pedipalps and it lacks the tufts (Clark 1994). Lacking tufts and orange palps, females are characterized by a rusty colored dorsal abdomen and a conspicuous white stripe below the anterior eyes (Barnes 1955; Kaston 1972).

In addition to morphological differences, the males differ in behavior during the initial phase (= phase I) of courtship (Clark 1994). The tufted morph stilts up on legs II–IV, raises and waves its first pair of legs back and forth and swings its abdomen side-to-side at an average distance of 9 cm from the female. The gray morph crouches in a prone posture, pointing legs I and II forward in a triangle-like configuration and sidles back and forth in front of the female at an average distance of 3 cm (Clark & Uetz 1993).

Previous studies of mate choice in *Maevia*

inclemens have demonstrated that females tend to choose the male they see move first, independent of male morphology (Clark & Uetz 1992) and that as a function of different courtship distances, males present females with visual signals that are similar in size (Clark & Uetz 1993). These studies suggested that the different courtship behaviors of the two male morphs might represent alternative reproductive strategies for exploiting a movement bias in the mate selection system. Although it is known that females tend to choose the male they see move first, little is known about other aspects of male courtship behavior that might have an effect on the levels of mating success. The objective of this study was to determine if the two different male morphs of *Maevia inclemens* achieve equal or different levels of mating success. Similar to a study by Fernandez & Ortega (1990), the number and duration of copulation events and the number of offspring produced by each morph was used as a measure of mating success. Additionally, we scored the latency of visual orientation by the female to a courting male and how copulation events were terminated.

METHODS

Mature male and penultimate female *M. inclemens* were captured at several field sites in the local Cincinnati, Ohio (Hamilton County) area by hand and sweep net during the spring breeding season in June of 1995 and 1996. Voucher specimens have been deposited in the natural history collection at Alma College (Alma, Michigan). Spiders were maintained in the lab at Alma College and housed in cylindrical plastic deli containers, measuring 12 cm (d) x 4 cm (h). A diet of domestic crickets (*Acheta domesticus*) and fruit flies (*Drosophila* sp.) was provided on a weekly basis, and water was available *ad libitum*.

All observations of courtship behavior occurred between June and July of 1995 and 1996. Males and females were paired in a rectangular plastic arena, measuring 30 cm (l) x 15 cm (w) x 3 cm (h). A center partition separated the individuals during an acclimation period of approximately three min. The inner sides were lightly coated with petroleum jelly to keep the spiders from climbing out and escaping. Each female was randomly paired with an individual male (Total $n = 55$

females; with $n = 26$ tufted males; and $n = 29$ gray males). To control for previous mating experience, only virgin females (assessed by a final molt) were used. After the center partition was removed, spiders were allowed to freely interact until copulation termination or until the female rejected the male, whichever came first. Because females that decamp may be soliciting males to follow, rejection was defined as the female running away from the male three times and trying to escape out of the arena. In the event of no courtship, the individuals were separated after 12 min and were not tested again.

Each pairing was videotaped using a Panasonic HD 5100HS video camera and a Panasonic AG-1970 VHS format videocassette recorder. Subsequent to videotaping, the male and female interactions were scored for behavior frequency and duration using the "Observer" (Noldus Corp.) behavioral analysis program. Each interaction was scored for the following: a) Courtship—whether the male courted the female; b) Orientation latency—latency to female visual orientation of the courting male; c) Mating attempt—male tried, but did not successfully mount the female; d) Copulation—whether the male successfully mounted and copulated with the female; e) Female receptivity—females were scored for signaling to the male by either leg tapping or body posturing (see Clark 1994); f) Copulation events—number of copulation events per male; g) Copulation duration—the amount of time for each copulation event; h) Copulation termination—a score was given for how the copulation ended i.e., did the female force the male to dismount by attempting to dislodge it; or, did the male dismount voluntarily; and, did the female prey upon the male. For statistical comparisons, the chi-square test was used to test for differences among frequencies and the Wilcoxon sign rank test was used test for differences between sample distributions (reported as sample means).

Subsequent to a successful mating, females were maintained in the laboratory and allowed to construct egg sacs. The number of offspring resulting from each pairing was counted at the time of dispersal from the maternal egg sac. Since only virgin females were used, the offspring were the direct result of the interactions observed in the laboratory.

RESULTS

There were a total of 55 male and female pairings; 26 with tufted males and 29 with gray males. There was no significant difference in the number of males that courted females; 23 (88%) of the tufted males courted and 26 (89%) of the gray males courted ($\chi^2 = 0.02$, $df = 1$, $P > 0.05$; Table 1a). Only males that courted females were used in further analysis of mating success.

For males that courted, the latency to female visual orientation of the courtship display was measured. For all instances where visual orientation by the female was discernable, a significant difference in latency between the two male morphs was found (tufted $\bar{x} = 12.9$ sec, $SD = 3.68$, $n = 20$; Gray $\bar{x} = 9.84$ sec, $SD = 6.2$, $n = 22$; Wilcoxon test; $z = 2.33$; $P < 0.02$ Table 1b). Since Clark & Uetz (1993) and Clark (1994) reported that the males initiate courtship from significantly different distances from the female, tufted $\bar{x} = 9$ cm and gray $\bar{x} = 3$ cm respectively, an additional analysis of orientation latency to the courtship display was conducted. Here, the distance from the female was partitioned into two zones that covered the typical courtship range of the different males. The close zone was typical of the gray morph and ranged from 0 to 8 cm from the female. The distant zone was typical of the tufted morph and ranged from 8 cm and greater (maximum of 30 cm due to the length of the arena). In the close zone, the mean latency of visual orientation by the female toward the gray morph was significantly less than for the tufted morph (tufted $\bar{x} = 11.5$ sec, $SD = 3.47$, $n = 10$; gray $\bar{x} = 5.9$ sec, $SD = 1.69$, $n = 15$; Wilcoxon test; $z = 3.73$; $P < 0.001$; Fig. 1). However, in the distant zone, the advantage shifted to the tufted morph where the mean orientation latency toward tufted males was significantly lower than for gray males (tufted $\bar{x} = 14.3$ sec, $SD = 3.49$, $n = 10$; gray $\bar{x} = 18.14$ sec, $SD = 3.28$, $n = 7$; Wilcoxon test, $z = 1.92$, $P < 0.05$; Fig. 1). Interestingly, there was not a significant difference in orientation latency when the tufted individuals that courted in the close zone were compared to those tufted individuals that courted in the distant zone (Wilcoxon test: $z = 1.59$, $P > 0.10$; Fig. 1). However, when the gray males that courted in the close zone were compared

Table 1. Summary of the measurements of mating success for the two male morphs of *M. inclemens*.

	Tufted	Gray	Test	df	p	Power
a) Males that courted (n = 55)	23/26 (88%)	26/29 (89%)	$\chi^2 = 0.02$	1	>0.88	0.05
b) Mean female orientation latency (per males that courted)	12.9 s + 3.68 SD	9.84 s + 6.2 SD	$z = 2.33$		<0.02	0.47
c) Mean Mating Attempt (per males that courted)	3.34 + 2.63 SD	2.53 + 2.26 SD	$z = 1.07$		>0.2	0.17
d) Number of Males to Copulate (per males that courted)	12/23 (52%)	14/26 (54%)	$\chi^2 = 0.014$	1	>0.90	0.05
e) Female Receptivity (per males that copulated)	10/12 (83%)	11/14 (78%)	$\chi^2 = 0.095$	1	>0.75	0.05
f) Mean Copulation Events (n = 59)	2.6 + 1.87 SD	1.9 + 0.82 SD	$z = 1.12$		>0.2	0.46
g) Mean Copulation Duration (n = 57)	5.6 s + 5.0 SD	5.1 s + 5.8 SD	$z = 0.71$		>0.4	0.07
h) Male Terminates Copulation (n = 52)	5/26 (19%)	3/26 (12%)	$\chi^2 = 0.59$	1	>0.44	0.05
i) Mean Offspring Produced	25.5 + 8.2 SD	24.9 + 8.3 SD	$z = 0.0$		>1.0	0.06

to those individuals that courted in the distant zone, there was a significant difference in latency to orient (Wilcoxon test: $z = 3.69$, $P < 0.001$; Fig. 1).

Of the males that courted, not all successfully copulated and males often attempted to mate several times before the female allowed the male to mount. However, there was no significant difference in the mean number of mating attempts between the two male morphs (tufted $\bar{x} = 3.34$, $SD = 2.63$, $n = 23$; gray \bar{x}

= 2.53, $SD = 2.26$, $n = 26$; Wilcoxon test: $z = 1.07$, $P > 0.2$; Table 1c). There was also not a significant difference in the number of males of either morph to copulate with female. For tufted males, 12 (52%) of the males copulated and for gray males, 14 (54%) of the males copulated with a female ($\chi^2 = 0.014$, $df = 1$, $P > 0.05$; Table 1d). Finally, females showed similar levels of receptivity towards the two male morphs. Of the males that copulated, 10 (83%) of the females' signaled receptivity to tufted males, and 11 (78%) of the females' signaled receptivity to the gray males ($\chi^2 = 0.095$, $df = 1$; $P > 0.05$; Table 1e).

Since males often copulated more than once, the number of times that an individual male copulated was scored. There was no significant difference in the mean number of times that either male morph copulated with the female (tufted $\bar{x} = 2.6$, $SD = 1.87$, $n = 32$; gray $\bar{x} = 1.9$, $SD = 0.82$, $n = 27$; Wilcoxon test: $z = 1.12$, $P > 0.2$; Table 1f). Likewise, there was no significant difference in mean copulation duration between the two male morphs (tufted $\bar{x} = 5.6$ sec, $SD = 5.0$, $n = 31$; gray $\bar{x} = 5.1$ sec, $SD = 5.8$, $n = 26$; Wilcoxon test: $z = -0.71$, $P > 0.4$; Table 1g).

Copulation generally terminated when the

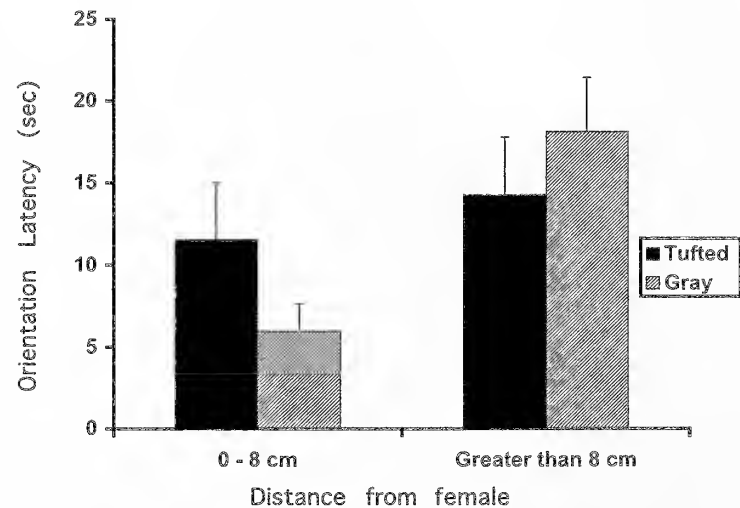


Figure 1.—Mean (+ SD) latency of female visual orientation to the courtship display of the two different male morphs of *Maevia inclemens* as function of distance. See text for statistical inference.

female tossed the male up, pushed him away and lunged in an attempt to capture the male. Females terminated copulation events significantly more often than males (female terminates = 85%; male terminates = 15%; $\chi^2 = 54.87$, $df = 1$, $P < 0.001$). However, there was no significant difference in copulation termination frequency between the two male morphs (tufted male terminated = 19%; gray male terminated = 12%; $\chi^2 = 0.59$, $df = 1$, $P > 0.05$; Table 1h). For all males that courted, one tufted male was preyed upon and no gray males were cannibalized in these observations.

As a final assessment of mating success, the number of offspring that dispersed from the maternal egg sac was counted. All females that copulated (tufted $n = 12$; gray $n = 14$) produced an eggsac and like most other assessments of mating success, there was no significant difference in the mean number of offspring produced by the two male morphs (tufted $\bar{x} = 25.5$ spiderlings, $SD = 8.2$, $n = 12$; gray $\bar{x} = 24.9$ spiderlings, $SD = 8.3$, $n = 14$; Wilcoxon test: $z = 0.0$; $P > 0.99$; Table 1i).

On a cautionary note, when there is failure to reject the null hypothesis, the possibility of a type II (β) error should be considered (Clark 1988). As a final analysis of the data, statistical power tests were conducted to determine the likelihood of making a type II error (see Cohen 1969). In general, the power results are consistent with our failure to reject the null hypothesis (summarized in Table 1). However, for (f) mean copulation events, the power results suggest some opportunity for a type II error.

DISCUSSION

In this study, mating success was measured in terms of time (i.e., latency of visual orientation by the female to a courting male and mating attempts); probable sperm transfer (i.e., copulation frequency and duration); displays of female sexual receptivity; risks associated with courtship and mating (i.e., orientation latency as a function of distance from the female and copulation termination); and lastly, the number of offspring produced by each male morph. With the exception of orientation latency as a function of distance, the results presented here indicate that the two male morphs of *M. inclemens* expend approx-

imately equal amounts of time (and perhaps energy) courting and mating and ultimately produce equal numbers of offspring.

Almost all individuals of both male morphs courted the female in whose presence they were placed. Males generally began courtship by performing the morph-specific phase I courtship display (see Clark 1994) and almost all males that courted attempted to mate at least one time. For a mating attempt, the male would typically perform a zig-zag dance display or phase II (see Clark 1994) and move close to the female, touch her with legs I and attempt to mount. If unsuccessful, the male would move away and continue the phase II zig-zag dance display and then reattempt to mate until the female accepted or ran away. If the female ran away, the male usually chased and attempted to resume courtship. Both male morphs attempted to mate with the female an average of three times before they mounted the female successfully. It is likely that during these mating attempts females were assessing some quality about the male, however, they did not appear to treat the male morphs differently. This finding is supported by the equal number of males of each morph that received a signal of receptivity from females. These results support earlier studies on female receptivity where it was reported that females are equally receptive to the two different male morphs (Clark & Uetz 1992, 1993). Although many individuals were not successful at mating, there was no difference in the number of males of either morph that copulated with the female.

Not only did the same number of males of each morph gain access to females; the number of copulation events was approximately the same for both male morphs. Likewise, the duration of copulation was similar for the males, where each morph copulated for approximately five sec per copulation event. Although sperm volume was not measured directly, these results suggest that the two male morphs are transferring approximately equal amounts of sperm to the female (Jackson 1980). Likewise, with similar levels of sperm transfer, the number of offspring fathered by the two male morphs was not significantly different.

The two male morphs also appear to experience similar levels of predation risk from females. Results presented here demonstrated

that females treated males equally with respect to copulation termination. In general, females ended a copulation event by attempting to toss the male off of her body. They did this by lifting their abdomen quickly and at the same time lifting the legs and lunging toward the male. Slow speed examination of videotapes revealed that females were attempting to capture the male while tossing it from their body. Both male morphs responded similarly by rapidly backing up (in less than a 1/30 sec) a centimeter or two from the female and then resuming phase II courtship.

Given the rather violent ending to mating, it might be expected that females would prey upon males more frequently. However, sexual cannibalism is relatively rare in this species. Clark (1992) and Clark & Uetz (1992) reported a frequency of approximately 2–3% of the males that court being preyed upon by the female. This is consistent with the current study in which one tufted morph was preyed upon. With such a small sample it is difficult to speculate on differences between the morphs. However, it is noteworthy that in this instance of sexual cannibalism, the tufted male had been performing phase I courtship approximately 4 cm from the female when she attacked. This suggests the possibility of different risks associated with morph-specific courtship displays as a function of distance from the female.

Another measure of risk associated with courtship display is the amount of time a male displays before being noticed by the female, or the latency of visual orientation. Since during phase I courtship males are attempting to attract female attention (Clark & Uetz 1992, 1993; Clark 1994) and the longer a male displays, the greater the risk associated with being spotted by visual predators. Although significantly different, overall, both males displayed for approximately similar amounts of time before the female visually oriented. The difference between the morphs becomes more apparent when courtship distance from the female was taken into account. At distances ranging from the female to 8 cm, gray males attracted female attention in significantly less time than tufted males within this same range. However, at distances ranging from 8–30 cm from the female (constrained by the length of the arena), tufted males attracted female attention in significantly less

time than gray males in the same range. Clark & Uetz (1993) reported that the perceptual area of the displaying male decreases as a function of distance from the female. Therefore, it is possible that it takes a female longer to orient to the gray male at a distance because the corresponding size of the males' image is decreased. Or, it may be that the species specific morphological cues, such as orange pedipalps and the stripe above the eyes, have become obscured at a distance. Regardless, at a distance, gray males must display significantly longer than tufted males to attract female attention, providing evidence for the benefits associated with courting females from two different distances.

The results presented in this study suggest that the two male morphs of dimorphic jumping spider, *M. inclemens*, attain equal levels of reproductive success. However, some studies of alternative male mating tactics suggest a frequency dependent selection mechanism, which maintains the polymorphism (Rubenstein 1980; Austad 1984). In light of the data presented here, such a mechanism for *M. inclemens* remains elusive. A more plausible explanation for the maintenance of the two *Maevia* male morphs is a mixed Evolutionarily Stable Strategy or ESS (Maynard Smith 1988) where the polymorphism is genetic (Clark 1992) and each morph has evolved its own unique tactic with equal fitness. It is likely that sexual selection plays a role in balancing the dimorphism (Gadgil 1972) and that the two male morphs of *M. inclemens* represent strategies for exploiting different courtship distances from the female. Further study on the role of the morph-specific courtship behaviors, as a function of distance from the female, is required.

ACKNOWLEDGMENTS

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**THE FIRST MYGALOMORPH SPIDER WITHOUT
SPERMATHECAE: *SICKIUS LONGIBULBI*,
WITH A REVALIDATION OF *SICKIUS*
(ARANEAE, THERAPHOSIDAE, ISCHNOCOLINAE)**

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ABSTRACT. The monotypic Brazilian genus *Sickius* Soares & Camargo 1948 is revalidated, rediagnosed, and tentatively transferred to the Ischnocolinae. The formerly unknown female of *S. longibulbi* Soares & Camargo 1948 is found to lack spermathecae. This unusual genital feature, not found in any other mygalomorph spider species, is described and discussed.

Keywords: *Sickius longibulbi*, Theraphosidae, Ischnocolinae, spermathecae, spider taxonomy

Soares & Camargo (1948) described the genus *Sickius* and the only species *S. longibulbi* Soares & Camargo 1948 based on a single male specimen from the eastern border of Rio das Mortes, Chavantina, State of Mato Grosso, Brazil. Raven (1985) placed it in synonymy with *Hapalotremus* Simon 1903 because it shares the conformation of the tibial spur and the associated bent metatarsus. However, the type was not located at that time (Raven 1985) and the synonymy was based on the original taxonomic description and published figures. No other study has been done so far on the genus.

Recent searches by the authors in the arachnid collections of Museu de Zoologia da Universidade de São Paulo resulted in the rediscovery of the holotype of *Sickius longibulbi*. Furthermore, collecting in several Brazilian localities resulted in many specimens belonging to this species, which allow us to revalidate the genus *Sickius* as well as to describe the so far unknown female of *S. longibulbi*. Unexpectedly, this species was found to lack spermathecae, a feature only found in a few spider species (Forster 1980; Uhl 1994), none of them belonging to the Mygalomorphae. The morphology of the female genital organ was carefully examined and described.

METHODS

Specimens are deposited in the following institutions: Museu de Zoologia da Universi-

dade de São Paulo, São Paulo, Brazil (MZUSP, Carlos Roberto F. Brandão); Instituto Butantan São Paulo, Brazil (IBSP, Rogério Bertani); Universidade de Brasília, Brasília, Brazil (UNB, Paulo Cesar Motta).

For genitalia and reproductive system studies, nine females preserved in 80% alcohol and one fresh dead specimen had their genitalia and reproductive organs (ovaries, oviducts, uterus internus and uterus externus) completely dissected under a stereoscopic microscope. Of these, two females had their genital tract examined in order to look for the site of sperm deposition: a preserved female was examined with large abdomen and well-developed oocytes, which was considered a sign of pregnancy; and another female was sacrificed and dissected 18 hours after copulation. Ovaries, oviducts, uterus internus and uterus externus were examined under a stereomicroscope and samples of structures resembling coenospermia were taken from oviducts and uterus internus lumen and mounted on slides. These structures were then analyzed and photographed with a Zeiss Axiophot light microscope.

In order to search for spermathecae in cast skins, exuvia of three specimens kept in the laboratory for three years and another seventy specimens kept for nine months were examined, reaching a total of 90 exuvia.

SEM micrographs of internal genitalia of

subadult male casting skin, and of a preserved female were taken after being sputter-coated with gold, and examined in a Zeiss DSM 940. Measurements are in mm.

The terminology used for legs spination is based on Petrunkevitch (1925), with modifications. The total number of spines were expressed for basal, median and distal regions on each article side (p = prolateral, r = retrolateral, v = ventral). Those spines on edges of distal sides are identified as "ap" to differentiate these spines, commonly concentrated on the distal article edges, from other spread over the distal area.

TAXONOMY

Genus *Sickius* Soares & Camargo

Sickius Soares & Camargo 1948:405; type species:

Sickius longibulbi Soares & Camargo 1948; by original designation.—Brignoli 1983:140.

Haplotremus Simon: Raven 1985:151 (synonymy, here rejected).—Platnick 1989:103.

Diagnosis.—Males can be distinguished from other ischnocolines by the characteristic shape of the male palpal bulb and tibial spur (Figs. 1–5) as well as by the presence of a metatarsal ventral spur (Figs. 4, 5). Females can be distinguished by the absence of spermathecae.

Description.—See description of type species.

Sickius longibulbi Soares & Camargo Figs. 1–9

Sickius longibulbi Soares & Camargo 1948:406, figs. 86–88, holotype male from eastern border of Rio das Mortes, State of Mato Grosso, Brazil, H. Sick collected, September/December 1946 deposited at MZUSP, No. E.814 C.1248, examined. Brignoli 1983:140.

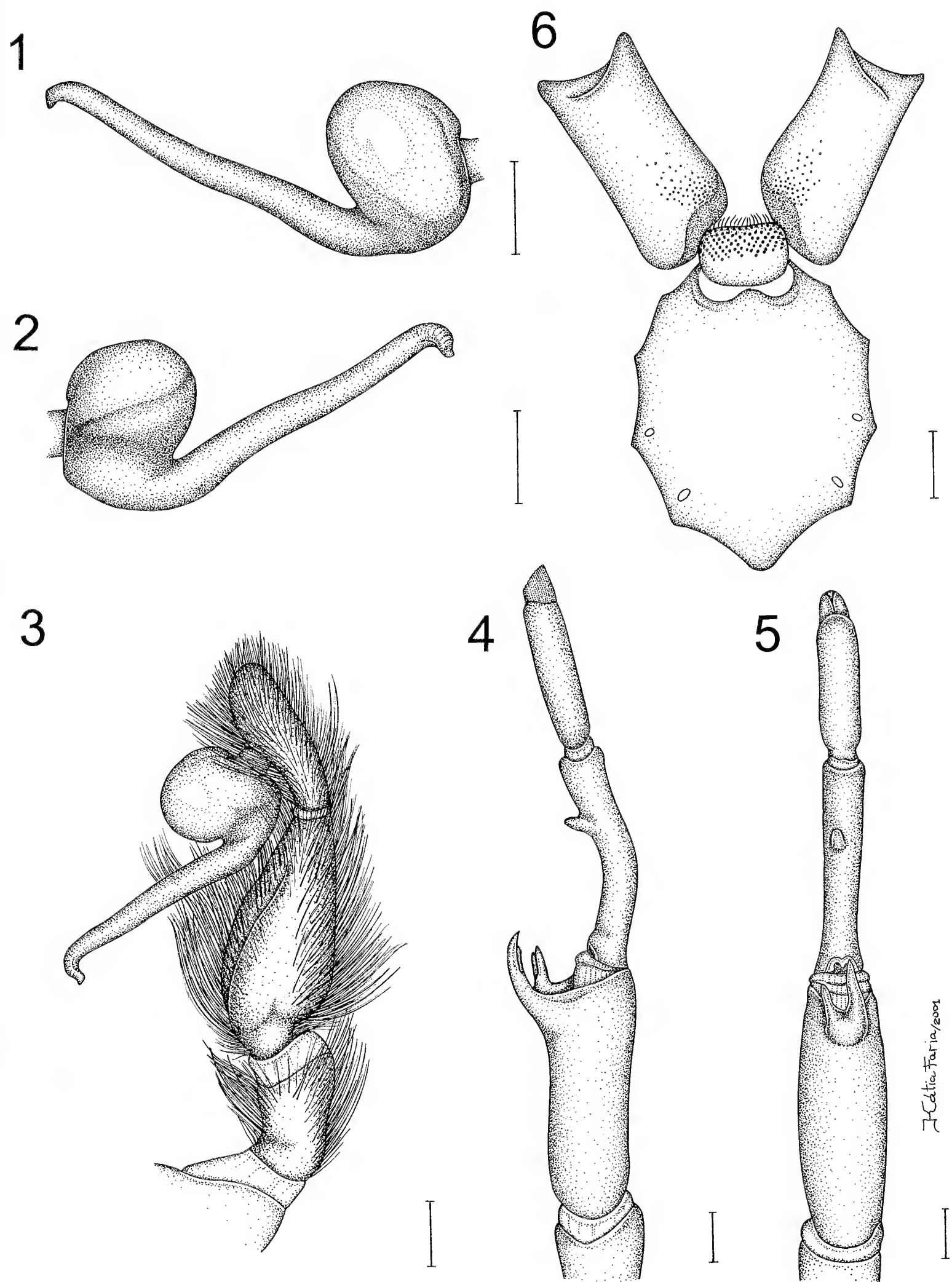
Haplotremus longibulbi: Raven 1985:151.

Diagnosis.—See diagnosis for the genus.

Description.—*Male*: (IBSP 8019, Paranaíba, Mato Grosso do Sul, Brazil, 3 November 1983, R.R. Silva). Total length with chelicerae: 22.0. Carapace: length 9.1, width 7.8. Eye tubercle: length 1.0, width 1.4. Labium: length 1.0, width 1.5. Sternum: length 4.0, width: 3.6. Cephalic region very low, hardly distinct. Thoracic striae undistinguishable. Fovea short, shallow, slightly recurved. Chelicerae without rastellum, basal segments with 9–10 teeth on promargin. Clypeus absent. Anterior

eye row procurved, posterior straight. Anterior median eyes rounded, same size as oval anterior lateral eyes. Posterior lateral and posterior median eyes oval, subequal, both shorter than anterior median and anterior lateral eyes. Labium with almost 100 cuspules on its anterior half. Maxilla subrectangular, anterior lobe distinctly produced into conical process, inner angle bearing numerous cuspules (> 50). Labiosternal suture broad. Sigilla: anterior pair not evident; second pair hardly visible; other very small, shallow, positioned about one diameter from margin. Posterior median spinnerets one-segmented, short; posterior lateral spinnerets three-segmented, basal segment shorter than median, both shorter than digitiform apical. Claw tufts present; superior tarsal claws without teeth. Tarsi I–IV scopulate, III, IV divided by narrow row of setae; metatarsi I–III scopulate along half their length, metatarsus IV ascopulate. Femur IV without retrolateral scopula. Stridulatory setae absent. Legs I: femur 7.5, patella 3.2, tibia 5.7, metatarsus 5.0, tarsus 3.2, total 24.6, II: 6.4, 3.8, 4.8, 4.3, 3.0, 22.3, III: 5.9, 3.0, 4.3, 5.0, 3.2, 21.4, IV: 8.0, 3.7, 6.7, 7.5, 3.5, 29.4. Spines: tarsi lacking spines. Palpal femur 0, patella 0, tibia v0–1–0; legs I lacking spines; II femur 0, patella 0, tibia v0–0–2(ap), metatarsus v1–0–1; III femur 0, patella 0; tibia v2–2–3ap, p1–1–1, r1–1–0, metatarsus v1–1–3ap, p1–1–1, r1–1–0; IV femur 0, patella 0, tibia v1–1–3(2ap), p1–1–0, r1–1–0, metatarsus v2–1–3ap, p1–1–1, r1–1–0. Tibia I thickened. Male spur with two closely positioned straight branches originating from common, raised base. Retrolateral branch longer than prolateral. Both branches narrow, tapering slightly to distal portion, bearing very narrow spine contiguous to each branch on internal face. Metatarsus I bent at basal portion, with ventral spur on distal third portion, touching laterally retrolateral branch of tibial spur when flexed. Male palpal bulb with short subtegulum, not extending down bulb. Bulb globose, narrowing abruptly, giving origin to very long embolus, longer than palpal tibia. Male palpal bulb keels absent. Urticating hairs absent. General color pattern golden-brown. Carapace, abdomen and legs covered with golden hairs. Leg rings and longitudinal stripes on patellae and tibiae hardly distinct.

Female: (IBSP 8693, Votuporanga, São Paulo, Brazil, July 1995, Palinger, F. leg., ova-



Figures 1–6.—*Sickius longibulbi*, male, IBSP 8019, Paranaíba, Mato Grosso do Sul, Brazil: 1. Left male palpal bulb, retrolateral view; 2. Same, prolateral view; 3. Left palp; 4. Left leg I, retrolateral view; 5. Same, ventral view; 6. Maxillae, labium and sternum. Scale lines = 1 mm.

J. C. Faria/2004

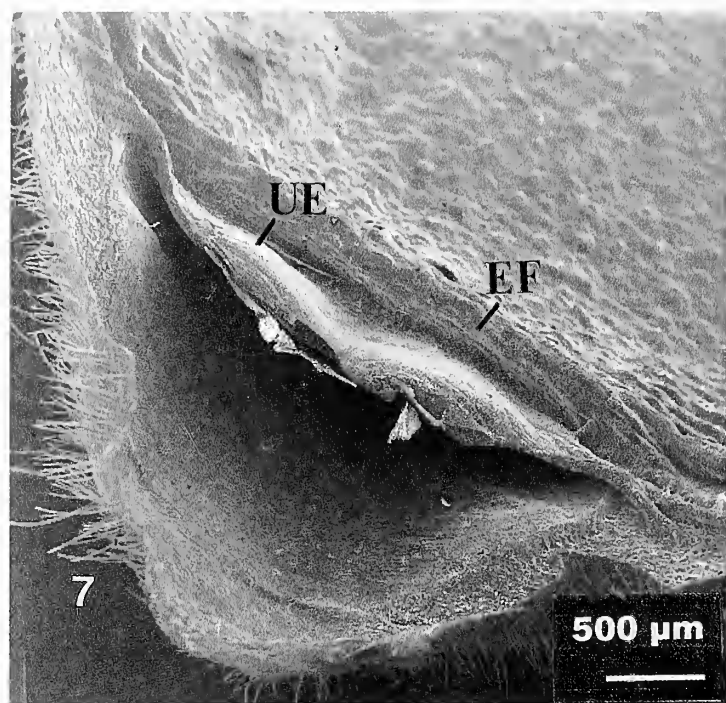


Figure 7.—*Sickius longibulbi*, female, internal genital area showing epigastric fold (EF) and uterus externus (UE).

ries and oviducts dissected). Total length with chelicerae: 25.7. Carapace: length 9.8, width 8.2. Eye tubercle: length 1.1, width 2.0. Labium: length 1.3, width 1.7. Sternum: length 4.5, width: 3.9. All characters as in male, except: both basal segments of chelicerae with 11 teeth on promargin; tarsi I–IV scopulate, all divided by narrow row of setae, more evident on tarsi III, IV; metatarsus IV scopulate on apical third; palpal tibia not thickened. Legs I: femur 8.0, patella 4.3, tibia 5.6, metatarsus 4.8, tarsus 2.7, total 25.4, II: 6.6, 4.0, 5.1, 4.3, 3.2, 23.2, III: 5.9, 3.5, 4.3, 5.4, 3.5, 22.6, IV: 8.2, 4.0, 6.9, 8.0, 3.5, 30.6. Spines: tarsi lacking spines. Palpal femur p0–0–1, patella 0, tibia v0–2–3ap; legs I femur p0–0–1, patella 0, tibia v0–0–2ap, metatarsus 0; II femur p0–0–1, patella 0, tibia v0–1–2ap, metatarsus v1–0–1ap; III femur r0–0–1, patella p1; tibia v1–0–3ap, p1–1–1, r0–1–1, metatarsus v1–1–3ap, p1–1–1, r0–1–1; IV femur r0–0–1, patella 0, tibia v2–1–3ap, p0–1–0, r1–1–0, metatarsus v2–1–3ap, p1–1–1, r1–0–1. Urticating hairs absent. Spermathecae absent.

Natural History.—*Sickius longibulbi* lives under rocks and fallen logs, sometimes digging shallow burrows that are filled with silk strands.

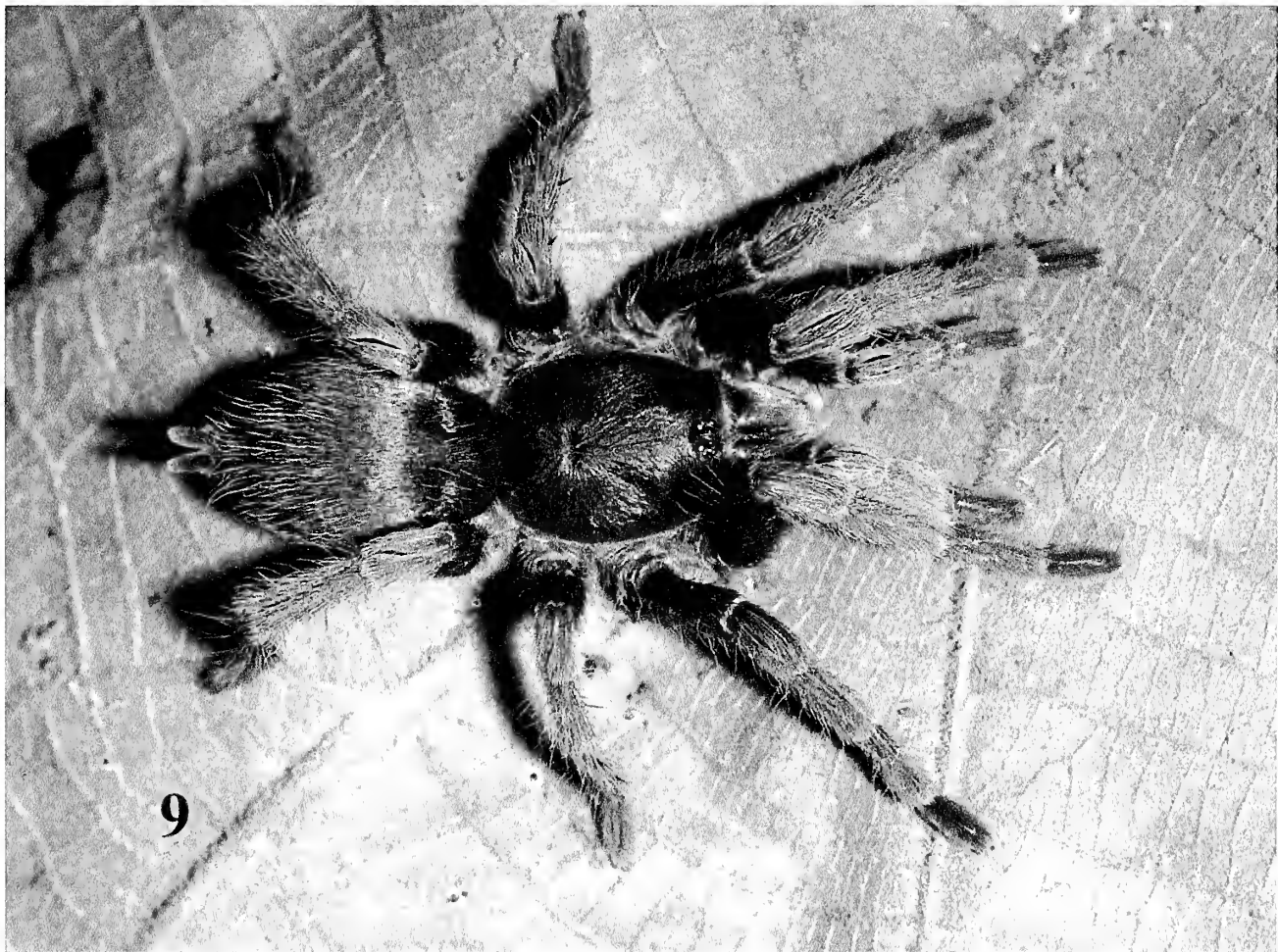
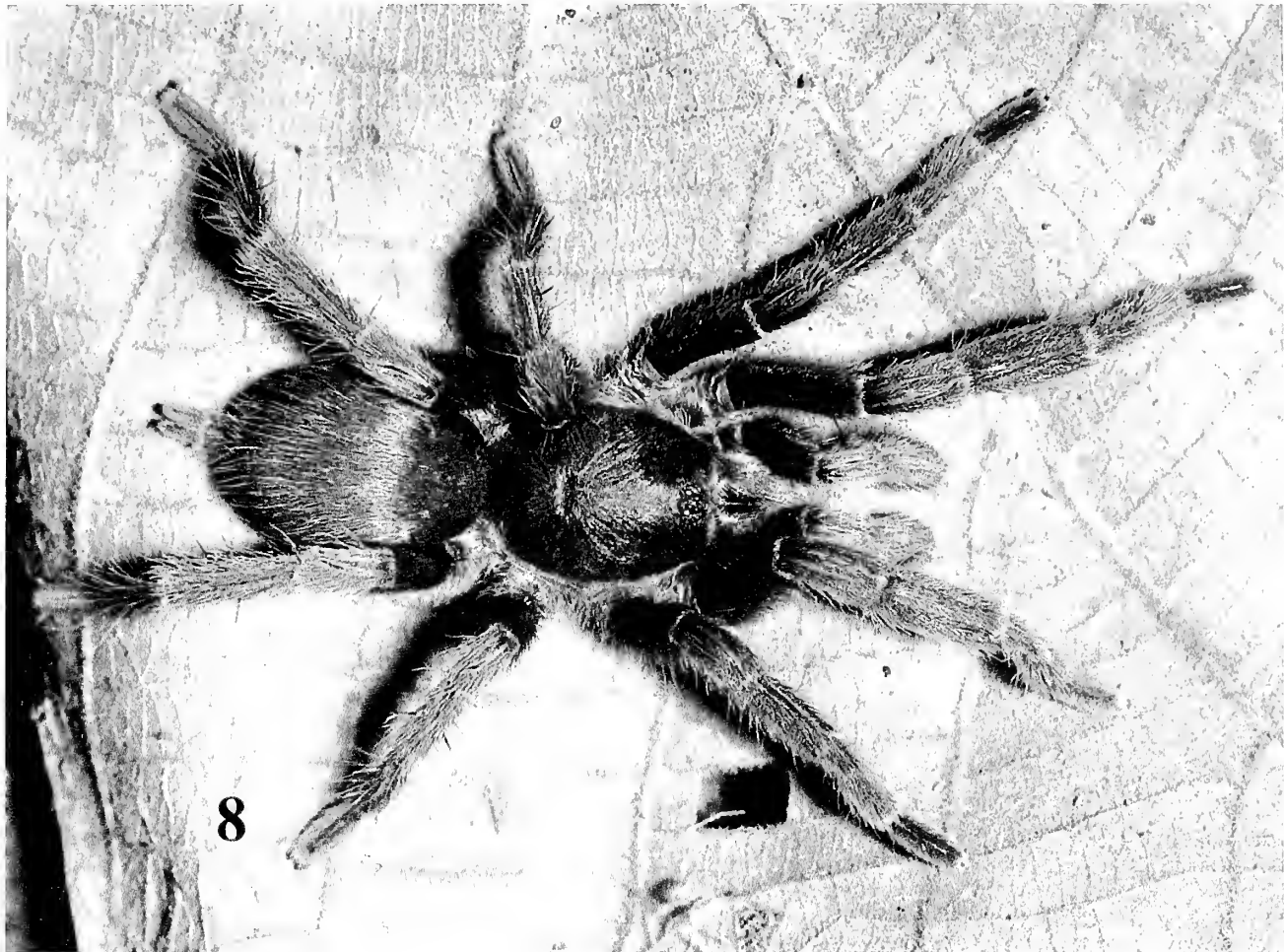
Remarks on the holotype.—The male copulatory bulbs, which are normally used in species identification, are missing. However, the unique conformation of the tibial apophysis, the presence of a metatarsal ventral

apophysis, and the original published figure of the male palpal bulb confirm the holotype's identity.

Soares & Camargo's (1948) description stated that in the holotype the sternum is much longer than wide and tapers slightly backwards, as confirmed by our examination of the specimen. However, this simply seems to be a condition occurring after ecdysis, since we have observed the same sternal shape modification in a few other specimens belonging to well-known species of the families Nemesiidae and Theraphosidae. The sternum in the other studied *S. longibulbi* specimens is just slightly longer than wide (Fig. 6).

Distribution.—*Brazil*: Eastern State of Mato Grosso to the Distrito Federal, and south to the States of Mato Grosso do Sul, State of São Paulo, and western State of Paraná, apparently following gallery forest of the valleys of the rivers Araguaya and Paraná as well as the Atlantic semi-deciduous forest of the States of São Paulo and Paraná.

Additional material examined.—*BRAZIL*: *Distrito Federal*: Brasília, inside termite's nest of *Armitermes euamignathus*, campus of Universidade de Brasília, 1 ♂, 3 ♀, 1 juvenile, 26 April 2000, P.C. Motta (UNB 985). *Mato Grosso do Sul*: Coxim, 1 ♂, 1 ♀, 20–21 December 1986, E.G. Soave (IBSP 8017). Piraputanga, 4 ♂, July 1999, A.D. Brescovit (IBSP 8059, 8820). Paranaíba, 1 ♂, 1 ♀, 21 January 1983, R.R. Silva (IBSP 8023, 8024); 1 ♂, 3 ♀, 25 August 1983, R.R. Silva (IBSP 8021, 8018). Bandeirantes Island, Paraná River, between Brasilândia, Mato Grosso do Sul State and Presidente Epitácio, São Paulo, 2 juveniles, 2 ♂, 1 ♀, 21 July 2000, R.P. Indicatti & M.S. Sebastião (IBSP 8709, 8718, 8681, 8717, 8819); 1 ♀ (dissected), July 2000, 1 ♀, August 2000, Equipe Resgate de Fauna (IBSP 8813, 8834); 4 juveniles, 3 July 2000, F. Cunha & C.A.R. Souza (IBSP 8635); 1 juvenile, 1 ♀ (dissected), 5 July 2000, C.A.R. Souza (IBSP 8719, 8818); 1 ♀, 1 juvenile, 3 August 2000, Candiani, D. & C.A.R. Souza (IBSP 8629); 1 ♂, 3 ♀ (IBSP 8720, 8710, 8627, 8631), 1 juvenile, 26 July 2000, I. Kny-sak & R. Martins (IBSP 8598). *São Paulo*: Guaraci, 1 male, 1 September 1993, Santos, J.J. (IBSP 8022). Votuporanga, 1 ♂, 2 ♀ (dissected), July 1995, Palinger, F. Ded. (IBSP 8821, 8814, 8816). Itirapina, 3 ♂, 2 ♀, 13 October 1999, 6 ♂, 12 October 1999, Oliv-



Figures 8–9.—*Sickius longibulbi*. 8. Male; 9. Female.

eira, M.E. (IBSP 8791, 8695, 8694, 8696, 8793). São Luis do Paraitinga, 1 ♂, 16 October 1983, Dardi, L. C. (IBSP 8020). Rosana, U.H.E. Rosana, Paranapanema River, 1 ♀, December 1986, Equipe de Resgate de Fauna (IBSP 8822). *Paraná*: Pinhão/Candói, U.H.E Segredo, Rio Jordão, 10 ♂, 6 juveniles, 14 ♀, 01 May 1996, Equipe de Resgate de Fauna

(IBSP 8810, 8823, 8812, 8808, 8829, 8811, 8826, 8824, 8825, 8828, 8827, 8809); 1 ♀ (dissected), 1996, Chagas-Junior, A. & Montingelli, G. (IBSP 8815).

Taxonomic remarks.—*Sickius* was synonymized with *Hapalotremus* because “they share the tibial apophysis conformation and the associated bent metatarsus” (Raven 1985). However, the type was not located at that time (Raven 1985) and the synonymy was based on published figures. *Sickius longibulbi* has a small subtegulum not extending down the bulb, and lacks both male palpal bulb keels and urticating hairs; therefore, it lacks all theraphosine synapomorphies (Raven 1985; Perez-Miles et al. 1996) and thus cannot be included in the theraphosine genus *Hapalotremus*. It is here included putatively in Ischnocolinae, because it lacks the synapomorphies for the remaining theraphosid subfamilies. Ischnocolinae is probably a paraphyletic assemblage considered as “incertae sedis” by Raven (1985).

The unique conformation of the male palpal bulb, the unusual shape of the male tibial apophysis and the presence of a metatarsal ventral apophysis on leg I of male (Figs. 1–5), as well as the absence of female spermathecae (Fig. 7), easily distinguishes the genus from other ischnocolines. On the other hand, these extremely derivative characters, not shared with any of the other ischnocoline genera, makes relationship comparisons difficult.

Female genital morphology.—Apart from some species of the families Liphistiidae, Diguettidae, Archaeidae and the Pholcidae (Forster 1980; Uhl 1994), all other spider species have spermathecae, which function to store sperm. In its simplest conformation, called haplogyne, a region or regions of the uterus externus (also called bursa copulatrix) is invaginated to form the receptaculum or spermatheca, which is surrounded by secretory tissue (Forster 1980). Both the uterus externus and spermathecae are chitinous structures, easily seen in dissected females, both adult and immature, of most species. In Mygalomorphae, in which females continue to molt after reaching maturity, the cuticular lining of the spermatheca is shed with the exuvium. In most theraphosid species, spermathecae appear early in development. Galiano (1984) stated that in *Acanthoscurria sternalis* Pocock 1903 the spermathecae are visible in the sixth

exuvium, when the prosoma is only 3 mm long, or 1/6 of the adult length, which occurs after 209–277 days of life. Stradling (1978) found spermathecae in *Avicularia avicularia* (Linnaeus 1758) specimens less than a year old and probably in the fifth or sixth instar. Therefore, it is clear that spermathecae are absent in *Sickius longibulbi*, since we did not find such a conspicuous structure in the dissected females or in any of the 90 exuviae examined (some of them belonging to females which constructed fertile eggsacs in captivity). Additionally, two females constructed fertile eggsacs 14 months after they were collected; and, interestingly, they had molted twice before eggsac construction. Because the molting process surely would lead to loss of the spermathecae together with the sperm mass in their contents (Foelix 1996), this supports the observation that spermathecae are absent in mature females. Contrary to females which bear the uterus externus (Fig. 7), immature males have a small genital opening (Fig. 10).

The question that arises then is, where is the sperm mass stored? In all living species lacking spermathecae, the families Liphistiidae, Diguettidae, Archaeidae and representatives of the Pholcidae, the sperm is stored in the uterus externus, a condition considered primitive (Forster 1980). In these cases, the wall of the uterus externus is associated with secretory glands which open through numerous pores across the surface of the genital tract (Forster 1980; Uhl 1994). In pholcids, spermatozoa are embedded in the female secretion, which serves to store and fix the sperm mass in a specific position within the uterus externus itself (Uhl 1994). In order to examine this possibility, two females had their genital tract examined to look for the site of sperm storage: a preserved female with large abdomen and well-developed oocytes, which was considered a sign of pregnancy; and a female which was sacrificed and dissected eighteen hours after copulation had taken place. Ovaries, oviducts, uterus internus and uterus externus were examined under a stereomicroscope and samples of structures resembling coenospermia were taken from oviducts and the uterus internus lumen. Under light microscopy it was confirmed that they were coenospermia, i.e., the multicellular sperm capsules found in mesothelae and theraphosid spiders (Alberti et al. 1986) (Figs. 11, 12). As

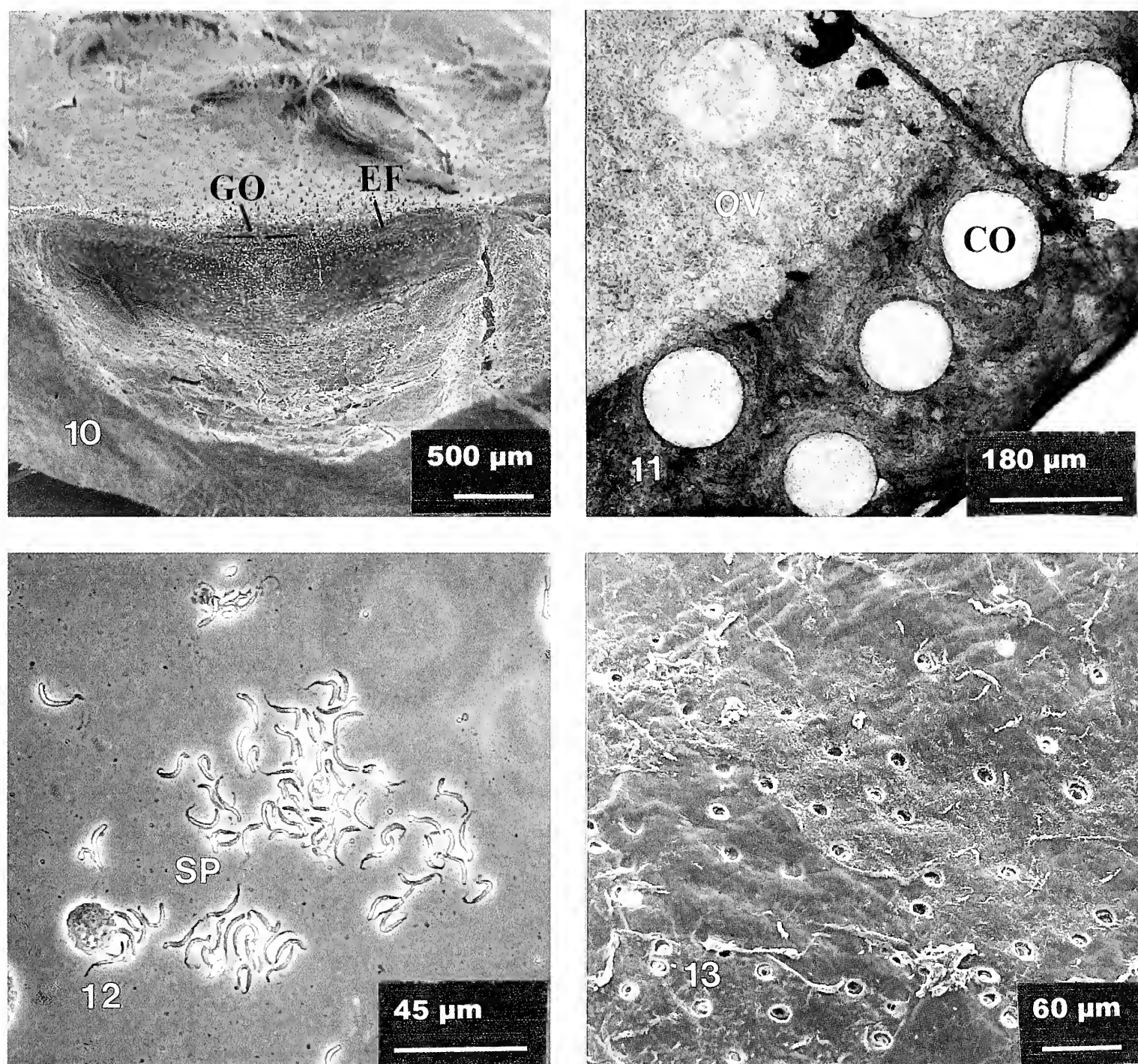


Figure 10–13.—*Sickius longibulbi*: 10. Male exuvium showing internal genital opening (GO) and absence of uterus externus. EF = epigastric fold; 11. Part of oviduct (OV) showing coenospermia (CO) inside its lumen; 12. Free spermatozoa (SP) from a ruptured coenospermium; 13. Female uterus externus posterior wall showing the presence of pores (P).

in *Pholcus phalangioides* (Fuesslin 1975) (Uhl 1994), the posterior wall of the uterus externus possesses pores (Fig. 13), but these were less numerous and more evenly spaced over the surface. However, unlike pholcids (Uhl 1994), no sperm mass was found fixed to the uterus externus wall. Detailed reports on mating behavior as well as on the morphology of female reproductive organs are in preparation by the authors.

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KEYS TO THE GENERA OF ARANEID ORBWEAVERS (ARANEAE, ARANEIDAE) OF THE AMERICAS¹

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ABSTRACT. This paper contains keys to the 65 genera of araneid spiders known from the Americas. These genera hold approximately fifteen hundred species found in the Americas. The key to females uses mostly artificial characters; the key to males uses diagnostic characters. There are four new synonyms and two new placements.

Keywords: Arachnida, Araneidae, taxonomy, keys

A challenge of taxonomy is to overcome the difficulties of determining common invertebrate animals. Correct determination is essential for most biological research. This key is intended to help specialists and nonspecialists determine genera of araneid orb weavers.

Simon (1895), who established many of the genera and groups of araneid genera, unfortunately did not provide complete keys to his groupings. A key to North American genera is found in Roth (1994). Keys to European genera are found in Heimer & Nentwig (1991) and Roberts (1995). There is a key to the subfamilies of African Araneidae by Dippenaar-Schoeman & Jocqué (1997). I have circulated a rough, unpublished key to genera of American species, to help curators search out loan specimens for my revisionary studies between 1983 and 1989. A key to Eurasian, African and Australian araneid genera is planned.

The 1,500 American species of the Araneidae are listed in several catalogs of spiders. Those described to 1938 are listed in Bonnet (1955–1959) and Roewer (1942). These catalogs have been updated, following Roewer's style, by Brignoli (1983) and Platnick (1989, 1993, 1997, 2001). The groups included in the Araneidae are controversial (Scharff & Codrington 1997). Here we consider the Araneidae in the limited sense, with the Tetragnathidae including *Nephila* and *Meta*, and the

Theridiosomatidae and Anapidae as separate families.

The Araneidae are ecribellate, entelegyne, three-clawed spiders, having eight eyes in two rows. The lateral eyes are usually adjacent and some distance from the medians; the four medians form a trapezoid (Figs. 28, 54). The posterior median and lateral eyes have a canoe-shaped tapetum, slender in posterior median eyes, with rhabdoms in parallel rows toward the median side (Homann 1950; Levi 1983, fig. 10). The height of the clypeus is usually less than two diameters of the anterior median eyes (Fig. 54). The labium is wider than long to square, distal edge swollen. The endites are only slightly longer than wide (Fig. 201). The abdomen is globose, overhanging the carapace (Figs. 8, 9) and with a colulus. Aggregate silk glands produce viscid silk. Legs usually have macrosetae, but lack trichobothria on femora and tarsi. Small to large size, 1–25 mm total length.

The female epigynum ventrally has a copulatory structure, often with a scape or lobe (Fig. 76). The openings are posterior (Fig. 77); or rarely, secondarily moved ventrally (Fig. 52). The posterior has three plates with the opening in the slits between the plates (Figs. 11, 77, 117). The male palpus is rotated within the cymbium, showing most sclerites to the side of the cymbium (Fig. 186), and with a radix (R in Figs. 191, 192), a median apophysis (M in Fig. 191, 192), and a paracymbium that is fused to the cymbium (P in Fig. 228). Most Araneidae build an orb web with viscid tangential threads.

Diagnosis.—Araneids differ from all other

¹ Dedicated to the late B.J. Kaston and V.R. Roth, whose efforts made it possible for non-taxonomists to determine North American spider genera and species.

Table 1.—Authors of American araneid genera: literature citations and index to figures. Figure numbers below 184 are for females, above 185 for males.

References to revisions		Illustrations in this paper
<i>Acacesia</i> Simon 1895	Glueck 1994	24, 287–290
<i>Acanthepeira</i> Marx 1883	Levi 1976	60, 61, 220, 221
<i>Actinosoma</i> Holmberg 1895	Levi 1995b	63–65, 255, 256
<i>Aculepeira</i> Chamberlin & Ivie 1942	Levi 1977b, 1991a	128–131, 199
<i>Allocyclosa</i> Levi 1999	Levi 1999	58, 59, 273, 274
<i>Alpaida</i> O.P.-Cambridge 1889	Levi 1988	72–77, 175–184, 189, 190, 260–262, 291, 292
<i>Amazononepeira</i> Levi 1989	Levi 1989, 1994	142, 143, 198, 309
<i>Araneus</i> Clerck 1757	Levi 1971b, 1973, 1975b, 1991a	91, 92, 152–157, 205–207, 307
<i>Argiope</i> Audouin 1826	Levi 1968	3, 237, 238
<i>Araniella</i> Chamberlin & Ivie 1942	Levi 1974b	147, 148, 185, 186
<i>Aspidolasius</i> Simon 1887	(not revised)	36, 37, 213, 214
<i>Bertrana</i> Keyserling 1884	Levi 1989, 1994	167–170, 303, 304
<i>Carepalxis</i> L. Koch 1872	Levi 1992a	53, 54
<i>Cercidia</i> Thorell 1869	Levi 1975a	7, 194
<i>Chaetacis</i> Simon 1895	Levi 1985	32, 47, 222, 223
<i>Colphepeira</i> Archer 1941	Levi 1978	69, 70, 316
<i>Cyclosa</i> Menge 1866	Levi 1977a, 1999	78–85, 263–265
<i>Cyrtophora</i> Simon 1864	Levi 1997b	56, 57, 275, 276
<i>Dubiepeira</i> Levi 1991	Levi 1991a	135–138, 195
<i>Edricus</i> O.P.-Cambridge 1890	Levi 1991b	35, 229, 230
<i>Enacrosoma</i> Mello-Leitão 1932	Levi 1996	55, 253, 254
<i>Encyosaccus</i> Simon 1895	Levi 1996	31, 247, 248
<i>Epeiroides</i> Keyserling 1885	Levi 1989	95, 96, 281–283
<i>Eriophora</i> Simon 1863	Levi 1971a	112–114, 192
<i>Eustala</i> Simon 1895	Levi 1977a	13–15, 208–210
<i>Gasteracantha</i> Sundevall 1833	Levi 1978, 1996	33, 34, 251, 252
<i>Gea</i> C.L. Koch 1843	Levi 1968	1, 241, 242
<i>Hingstepeira</i> Levi 1995	Levi 1995b	97–99, 293, 294
<i>Hypognatha</i> Guérin-Méneville 1840	Levi 1996	29, 30, 217–219
<i>Hypsosinga</i> Ausserer 1871	Dondale et al. (in press)	102, 103, 203
	Levi 1972, 1975b	
<i>Kaira</i> O.P.-Cambridge 1889	Levi 1977b, 1993d	8–12, 93, 94, 313

Table 1.—Continued.

References to revisions		Illustrations in this paper
<i>Kapogea</i> Levi 1997	Levi 1997b	6, 299, 300
<i>Larinia</i> Simon 1874	Harrod et al. 1991	149–151, 204
<i>Larinioides</i> di Caporiacco 1934	Levi, 1974b	132–134, 187, 188
<i>Lewisipeira</i> Levi 1993	Levi 1993c	139–141, 305, 306
<i>Madrepeira</i> Levi 1995	Levi 1995b	126, 127, 197
<i>Mangora</i> O.P.-Cambridge 1889	Levi 1975a	2, 317
<i>Manogea</i> Levi 1997	Levi 1997b	5, 297, 298
<i>Mastophora</i> Holmberg 1876	Levi (in press)	25–27, 314, 315
<i>Mecynogea</i> Simon 1903	Levi 1997b	4, 239, 240
<i>Metazygia</i> FP.-Cambridge 1903	Levi 1995a	16–18, 158–163, 211, 212, 308
<i>Metepeira</i> FP.-Cambridge 1903	Piel 2001	120–122, 196
<i>Micropeira</i> Schenkel 1953	Levi 1995b	164–166, 310
<i>Micrathena</i> Sundevall 1833	Levi 1985	44–46, 224–228
<i>Molinaranea</i> Mello-Leitão 1940	Levi 2001	123–125, 296
<i>Neoscona</i> Simon 1864	Berman et al. 1971, Levi 1993a	108–111, 193
<i>Nicolepeira</i> Levi 2000	Levi 2001	48, 49, 104, 105, 216, 266, 267, 279, 280
<i>Ocrepeira</i> Marx 1883	Levi 1976, 1993b	115–119, 295
<i>Parawixia</i> FP.-Cambridge 1904	Levi 1992b	86, 87, 191, 231, 232, 270–272
<i>Pozonia</i> Schenkel 1953	Levi 1993b	22, 23, 284–286
<i>Pronous</i> Keyserling 1881	Levi 1995b	42, 43, 243, 244
<i>Rubrepeira</i> Levi 1992	Levi 1992a	71
<i>Scoloderus</i> Simon 1887	Levi 1976, Traw 1996	38, 39, 235, 236
<i>Singa</i> C.L. Koch 1863	Levi 1972, 1975b	100, 101, 201, 202
<i>Spilasma</i> Simon 1895	Levi 1995b	19, 301, 302
<i>Spinepeira</i> Levi 1995	Levi 1995b	62
<i>Taczanowskia</i> Keyserling 1880	Levi 1997a	20, 21, 277, 278
<i>Tatepeira</i> Levi 1995	Levi 1995b	144–146, 200
<i>Testudinaria</i> Taczanowski, 1879	Levi (in press)	28, 311, 312
<i>Verrucosa</i> McCook, 1888	Levi 1976	88–90, 257–259
<i>Wagneriana</i> FP.-Cambridge 1904	Levi 1976, 1991b	66–68, 268, 269
<i>Wittica</i> O.P.-Cambridge 1895	Levi 1986a	51, 52, 245, 246
<i>Wixia</i> O.P.-Cambridge 1882	Levi 1993b	40, 41, 233, 234
<i>Xylethrus</i> Simon 1895	Levi 1996	50, 249, 250
<i>Zygiella</i> FP.-Cambridge 1902	Dondale et al. (in press)	106, 107, 171–174, 215
	Levi 1974a, 2001	

families by having (with the exception of *Cyclosa*, *Zygiella*) a modified canoe-shaped tapetum in the posterior median eyes (Levi 1983, fig. 10; Coddington 1986). Palpi of araneid males differ from those of theridiids, tetragnathids and linyphiids by having the palpal bulb rotated (Fig. 191; Coddington 1986), the paracymbium attached to the cymbium (P in Fig. 228), and the presence of a radix (R) and median apophysis (M in Fig. 191). Larger size males may have a tooth on the endite and a hook on the distal margin of the first coxa (Fig. 201), not found in related families.

Araneid females differ from theridiids by having a colulus, lacking the comb-shaped setae on the fourth legs, and having the labium with a distal swelling. They differ from linyphiids by having the clypeus usually not higher than two diameters of the anterior median eyes (Fig. 54), often having a condyle on the outside base of the chelicerae (Fig. 36), and having the epigynal openings on the posterior face of the epigynum (Figs. 116, 117, 136, 137). Araneid females differ from tetragnathids by sometimes having a scape on the epigynum (Fig. 129), having a condyle on the outside base of the chelicerae, having a square to wider than long labium, endites only slightly longer than wide (as in male, Fig. 201) and always lack trichobothria on the fourth femur, while tetragnathids lack the condyle, have a longer than wide labium, longer endites, and may have trichobothria on the fourth femur.

Of the 65 genera of Araneidae found in the Americas, the males of two (*Rubrepeira*, *Spinepeira*) are not known. For one genus, *Carepalxis*, only males of the Australian species are known. Ten genera are monotypic (*Actinosoma*, *Allocyclosa*, *Aspidolasius*, *Colphepeira*, *Encyosaccus*, *Epeiroides*, *Madrepeira*, *Rubrepeira*, *Wixia*, *Spinepeira*), and in one genus, *Spinepeira*, the female is known from only one specimen.

Although they are listed in the catalogs in the family Araneidae, several genera are not included in the keys because they are synonyms or misplaced. They are listed in the appendix.

Use of Keys.—There are four keys here, two for females, and two for males. The first of each is a speed key, a shortcut to the detailed second key, and will guide the user to a number at the start of a couplet of the second key. The numbers in parenthesis at the start of a couplet denote the originating couplet.

Keys are supposed to have “all or nothing” characters, but it is difficult to find such characters that are easily visible and are diagnostic for females as well as for males. As a result a specimen may key out to the correct genus in more than one couplet. Because males have more characters important in diagnosis, the male key is more accurate. The males of many species are minute, less than 3 mm. The male key uses genital characters for which a microscope with a magnification of 100–150 x is needed, as well as good reflected lighting, and a black, non-reflective background, and the specimens must be kept completely submerged in ethanol. The male palpus may have to be amputated in order to view its structure (but should always be kept in a smaller vial in the same vial with the remaining specimen). This is an artificial key. Characters that unite groups here may or may not be synapomorphies.

METHODS

Conventions used for keys.—All illustrations of palpi are left ones. Authors of generic names and references are cited in Table 1. Definitions used are: A “spine” is a pointed, cone-shaped, immovable protrusion, while a “macroseta” is a large, often movable seta. Other terms used can be identified by the cited illustrations: base of epigynum, swelling, tubercles, scape, lobe, keel, hump, and ridge.

Abbreviations: A = terminal apophysis; AME = anterior median eye; C = conductor; ca. = about; E = embolus; LE = lateral eyes; max. = maximum size; M = median apophysis; P = paracymbium; PE = posterior eyes; PLE = posterior lateral eyes; PM = parame-dian apophysis; PME = posterior median eyes; R = radix; sp. = species; Y = cymbium.

KEYS FOR FEMALES

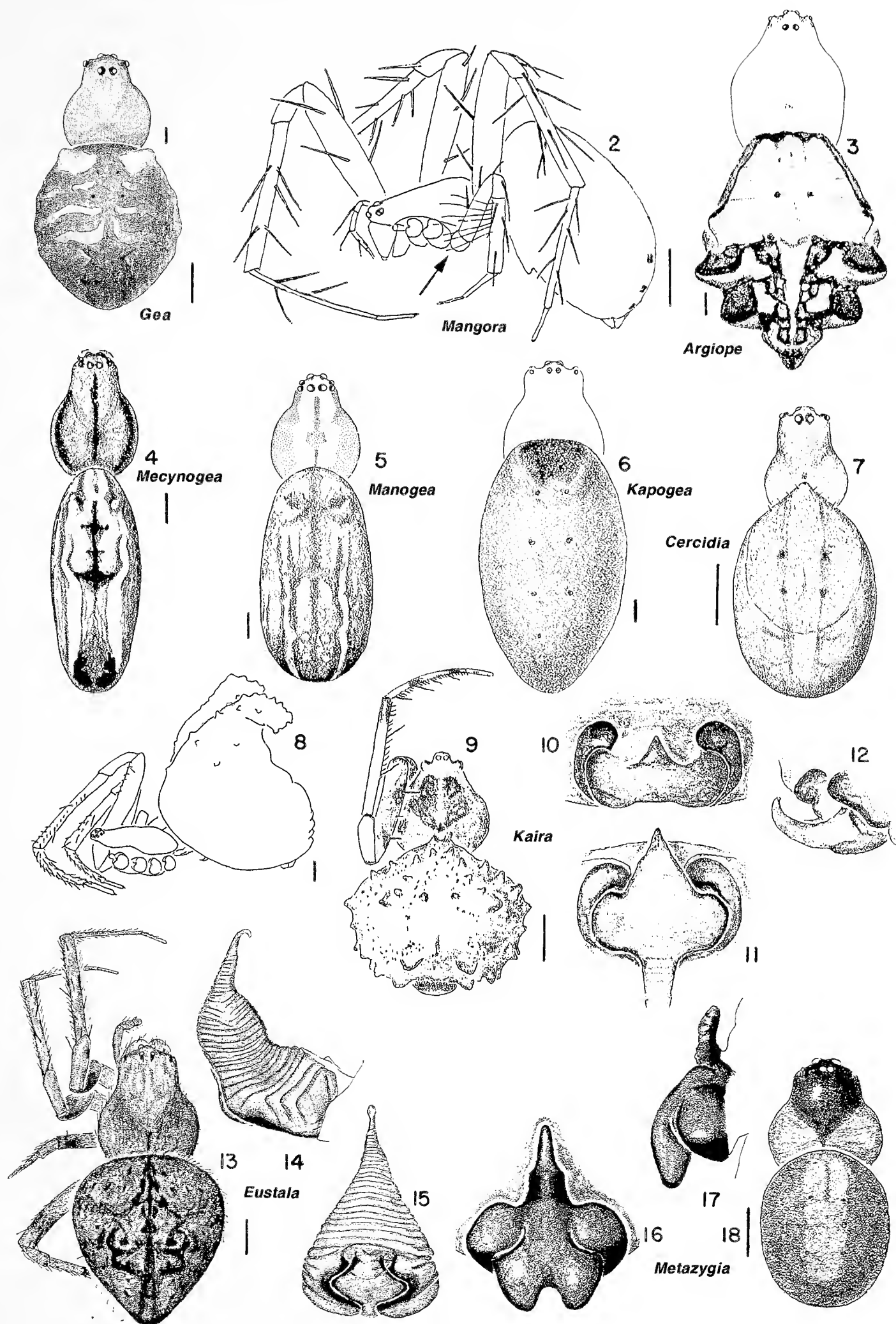
SPEED KEY FOR FEMALES

- 1 Third tibia with anterior, feathery trichobothria (Fig. 2). Go to 1 in key for females, or if not to 2 below.
- 2(1) Posterior eye row procurved (lateral eyes anterior to medians, Fig. 1) or straight (Fig. 6). Go to 2 in key, or if not to 10 below.
- 10(2) Epigynum with scape projecting anteriorly (Figs. 14, 15). Go to 10 in key, or if not to 13 below.
- 13(10) Cephalic width less than half width of thoracic region (Fig. 19). Go to 13 in key, or if not to 18 below.
- 18(13) Carapace with cephalic region as wide as thoracic (Figs. 30, 31, 34, 37), with tubercles (Figs. 25, 27), bulges, spines or extensions (Figs. 32, 35–37). Go to 18 in key, or if not to 34 below.
- 34(18) Abdomen with more than one pair of humps or tubercles, with extra tubercles, spines, sclerites or extending posteriorly (Figs. 44, 48, 51). Go to 34 in key, or if not to 55 below.
- 55(34) Abdomen wider than long (Figs. 88, 91, 93, 96). Go to 55 in key, or if not to 59 below.
- 59(55) Abdomen cylindrical (Figs. 97, 100). Go to 59 in key, or if not to 62 below.
- 62(59) Epigynum flat, without scape, lobe or ridge (Figs. 102, 105, 106). Go to 62 in key, or if not to 66 below.
- 66(62) Epigynum with scape (Figs. 109, 113, 122). Go to 66 in key, or if not to 86 below.
- 86(66) Epigynum with ridge or lobe (Figs. 159, 163, 172, 176). Go to 86 in key.

KEY FOR FEMALES.

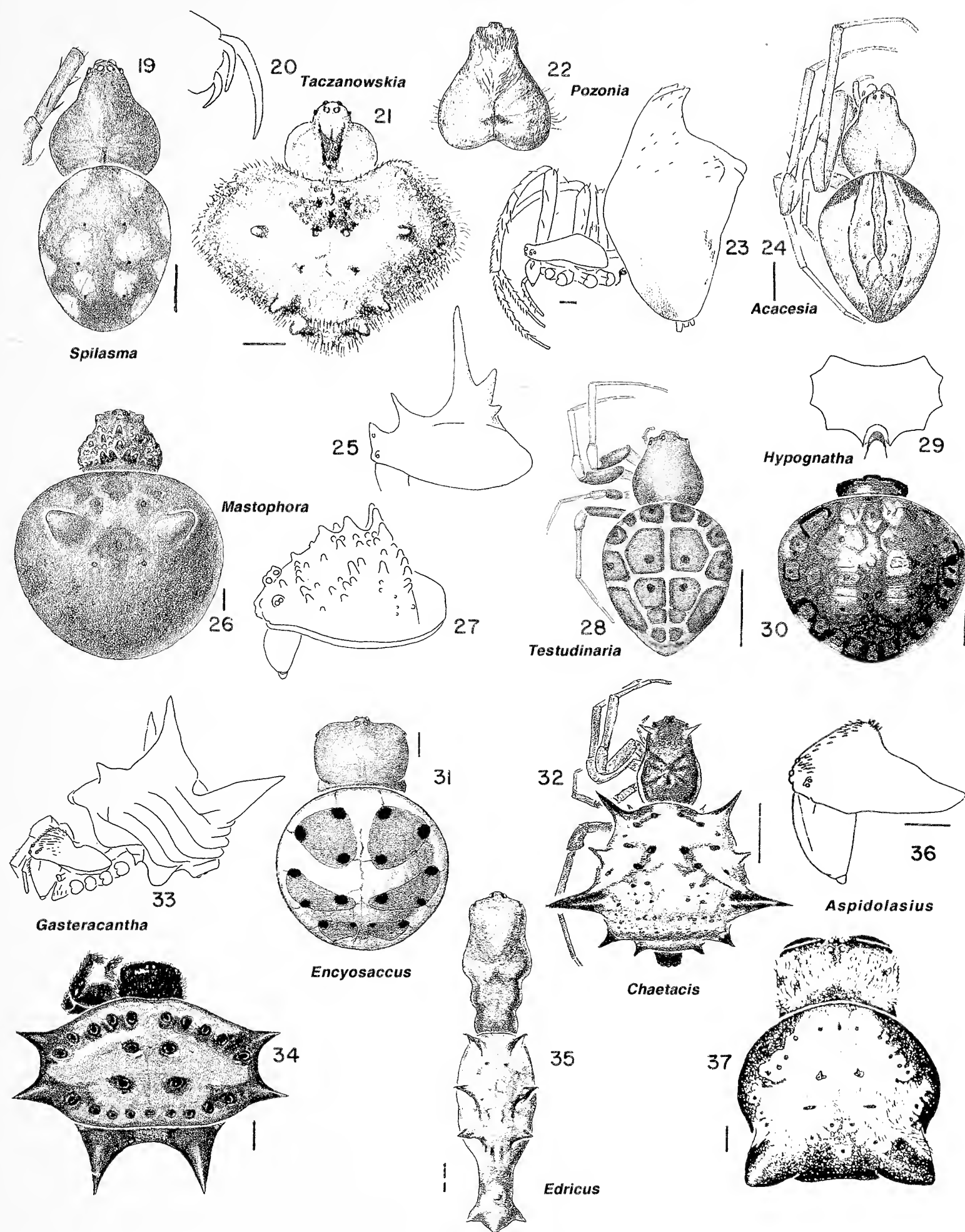
- 1 Third tibia with anteriorly facing, feathery trichobothria; high thoracic region of carapace (arrow Fig. 2); max. ca. 13 mm; ca. 20 sp., E Canada to Argentina, W Indies *Mangora*
- Third tibia without trichobothria (Figs. 13, 45) 2
- 2(1) PE row procurved (LE anterior to ME, Figs. 1, 3) or straight (Figs. 5, 6) when viewed from above 3
- PE row recurved, LE posterior to ME, or straight (Figs. 9, 13, 18) 10
- 3(2) Abdomen oval with scutum, anteriorly pointed, and bearing a line of about 8 macrosetae (Fig. 7); max. 5 mm; holarctic, or introduced to NE U. S. *Cercidia prominens*
- Abdomen otherwise (Figs. 3–6) 4
- 4(3) PE row procurved (Figs. 1, 3, 4) 5
- PE row straight (Figs. 5, 6) 8
- 5(4) Carapace with median black line and black sides of thoracic region (Figs. 4, 5); abdomen cylindrical (Fig. 4, 5); web horizontal 6
- Carapace without black line; abdomen oval to shield-shaped (Figs. 1, 3); web vertical 7
- 6(5) Abdomen with distinctive dorsal, white bands and with dark w-shaped mark in middle (Fig. 4); epigynum sclerotized; max. 12 mm; 9 sp., SE U. S. to Chile, Argentina, W Indies *Mecynogea*
- Abdomen with white bands but without w-shaped mark (Fig. 5); epigynum weakly sclerotized; max. 8 mm; 3 sp., Mexico to Venezuela *Manogea*
- 7(5) PME closer to each other than to LE (Fig. 3); max. 26 mm; 6 sp., Canada to Chile, W. Indies *Argiope*
- PE equally spaced (Fig. 1); max. 6 mm; U. S. to Argentina, introduced from SW Pacific? *Gea heptagon*
- 8(4) PME closer to each other than to LE (Fig. 6); lateral eyes separated by their diameter; abdomen shield-shaped (Fig. 6); web horizontal; max. 25 mm; 4 sp., Mexico to Argentina, W Indies. *Kapogea*
- PE equally spaced (Fig. 5); lateral eyes touching; abdomen oval to cylindrical (Fig. 5) 9

9(8) Carapace with median dusky line; sides of thoracic region dusky; abdomen cylindrical to oval (Fig. 5); web horizontal; max. 15 mm; Panama to N Argentina . . . *Manogea porracea*
— Carapace with median duskiness, sides of thorax yellowish (Fig. 171); abdomen oval (Fig. 171); vertical web, with viscid spirals missing in sectors below retreat; max. 9 mm; 5 sp., Alaska to U. S., introduced in Argentina, Chile . . . (in part) *Zygiella*
10(2) Epigynum with scape projecting anteriorly from its base (Figs. 10–12, 14–17) . . . 11
— Epigynum otherwise (Figs. 49, 52, 61, 70) . . . 13
11(10) Scape usually annulated (Figs. 14, 15); PME face dorsolaterally (Fig. 13); abdomen often with humps and triangular (Fig. 13), venter often with median white line; ; max. 15 mm; ca. 100 sp., Canada to Argentina, W Indies . . . *Eustala*
— Scape smooth (Figs. 10–12, 16); PME face dorsally (Figs. 9, 18); abdomen otherwise; . . . 12
12(11) Scape sclerotized, blunt (Figs. 16, 17); abdomen oval, widest in middle without humps; carapace glabrous with black cephalic region, PME adjacent, (Fig. 18); max. 12 mm; 88 sp., SE U. S. to Argentina, W Indies . . . (a few) *Metazygia*
— Scape pointed, not sclerotized (Figs. 10–12); abdomen with humps, tubercles (Figs. 8, 9); carapace setose; PME separated by their diameter; distal ends of first legs with setae and macrosetae (Figs. 8, 9); max. 14 mm; 14 sp., E U. S. to N Argentina, W Indies. . . (a few) *Kaira*
13(10) Cephalic width less than half width of thoracic region (Figs. 19, 21, 22, 24, 85) . . . 14
— Width of cephalic region one half or more of width of thoracic region (Figs. 26, 28, 30, 44) . . . 18
14(13) Abdomen wider than long, with tubercles (Fig. 21); tarsal claw, of first and second leg, spear-like, elongated (Fig. 20); max. 6 mm; 4 sp., Colombia to S Brazil . . *Taczanowskia*
— Abdomen longer than wide (Figs. 19, 23, 24, 85); tarsal claws of equal length . . . 15
15(14) Abdomen much longer than wide, with two anterior tubercles, and attached to pedicel at its posterior half (Fig. 23); max. 14 mm; 3 sp., S Mexico to S Brazil, W Indies . . *Pozonia*
— Abdomen without anterior, dorsal tubercles, usually attached to pedicel in middle or anterior half (Figs. 19, 24, 85) . . . 16
16(15) Abdomen pointed, extended and beyond spinnerets into a tail (Fig. 85); PME adjacent; max. 12 mm; 51 sp., Alaska to S Argentina, W Indies (some) . . . *Cyclosa*
— Abdomen without posterior extension, oval; PME separated (Figs. 19, 24) . . . 17
17(16) Abdomen with six pairs of dorsal, white patches on red (Fig. 19); max. 9 mm; 3 sp., Honduras to Rio de Janeiro State, Brazil . . . *Spilasma*
— Abdomen with two pairs of parallel black lines, their anterior and posterior end approaching midline (Fig. 24); 8 sp., E U. S. to N Argentina, W Indies . . . (in part) *Acacesia*
18(13) Carapace modified: with cephalic region as wide as thoracic, with tubercles (Figs. 25–27), spines (Fig. 32), macrosetae (Fig. 66), elongated (Fig. 35) or carapace bulging (Figs. 34–41) . . . 19
— Carapace without these modifications (Figs. 55, 56, 71) . . . 34
19(18) Carapace elongated, posteriorly drawn out (Fig. 35); max. 18 mm; 2 sp., Mexico to Ecuador . . . *Edricus*
— Carapace without posterior elongation (Fig. 26, 32) . . . 20
20(19) Cephalic region as wide or wider than thoracic (Figs. 30, 31, 34, 37) . . . 21
— Cephalic region narrower than thoracic (Figs. 28, 39) . . . 24
21(20) Abdomen entire, round or oval, glossy without spines or bulges (Figs. 30, 31) . . . 22
— Abdomen with spines or bulges, wider than long (Figs. 33, 34, 37) . . . 23
22(21) Sternum with a posterior median notch holding projection from abdomen (Fig. 29); abdomen with pattern of tortoise-like scutes (Fig. 30); max. 8 mm; 35 sp., Mexico to N Argentina . . . *Hypognatha*
— Sternum without notch; abdomen orange with six or more discrete, black patches (Fig. 31); max. 10 mm; upper Amazon . . . *Encyosaccus sexmaculatus*



Figures 1–18.—Females: 1. *Gea heptagon* (Hentz 1850), dorsal. 2. *Mangora maculata* (Keyserling 1865), lateral. 3. *Argiope argentata* (Fabricius 1775), dorsal. 4. *Mecynogea lemniscata* (Walckenaer 1841), 9dorsal. 5. *Manogea porracea* (C.L. Koch 1839), dorsal. 6. *Kapogea sellata* (Simon 1895), dorsal. Fig. 7. *Cercidia prominens* (Westring 1851), dorsal. 8, 10–12. *Kaira altiventer* O. P.-Cambridge 1889; 8. lateral; 10–12. Epigynum; 10. Ventral; 11. Posterior; 12. Lateral. 9. *Kaira shinguita* Levi 1993, dorsal. 13–15. *Eustala anastera* (Walckenaer 1841); 13, Dorsal; 14, 15. Epigynum; 14. Lateral; 15. Ventral. 16–18. *Metazygia yobena* Levi 1995; 16, 17. Epigynum; 16. Ventral; 17. Lateral; 18. Dorsal. Scale lines = 1mm.

23(21) Abdomen with two or three pairs of large spines (Figs. 33, 34); max. 8 mm; SE U. S. to Argentina, W Indies *Gasteracantha cancriformis*
— Abdomen with two posterior bulges; (Fig. 37); max. 11 mm; Venezuela to Bolivia ..
..... *Aspidolasius branicki*
24(20) Carapace with denticles around border and spines near lateral eyes (Fig. 32); max. 6 mm; 9 sp., S Mexico to Paraguay *Chaetacis*
— Carapace without denticles, without spines near lateral eyes (Figs. 31, 36) 25
25(24) Carapace high and with many tubercles (Figs. 25–27); abdomen wider than long; max. ca. 16 mm; 45 sp., NE U. S. to Argentina *Mastophora*
— Carapace with at most only two tubercles, two macrosetae; abdomen various shapes (Figs. 46, 66) 26
26(25) Center of thoracic region with two macrosetae (Fig. 66); abdomen longer than wide with 4 to 6 pairs of tubercles and posterior median tubercles (Fig. 66); max. 16 mm; 39 sp., SE U. S. to Argentina, W Indies (in part) *Wagneriana*
— Carapace without macrosetae. 27
27(26) Fourth femur longer than first (Fig. 45); Carapace with dimples, light rims and/or thoracic region swollen (Fig. 46); book lung covers usually with stridulating grooves (Fig. 47); abdomen with paired spines (Figs. 44, 45); max. 13 mm; 104 sp., S Canada to Argentina, W Indies (in part) *Micrathena*
— Fourth femur shorter or equal to first (Fig. 78); book lung covers without stridulating surface 28
28(27) Abdomen attached to prosoma at its middle or posterior (Figs. 38, 41) 29
— Abdomen attached at its anterior end to pedicel 30
29(28) Height of clypeus 3–4 diameters of the anterior median eye (Fig. 40) and abdomen projecting anteriorly above carapace (Fig. 41); max. 8 mm; Guyanas to Bolivia
..... *Wixia abdominalis*
— Height of clypeus at most two and one-half diameters (Fig. 38); abdomen not projecting anteriorly (Fig. 39); max. 5 mm; 5 sp., Florida to N Argentina, W Indies *Scoloderus*
30(28) Thoracic region much higher than cephalic (Figs. 46, 82); abdomen often with tubercles (Fig. 85), elongated and pointed behind spinnerets (Fig. 79, 80); max. 12 mm; 51 sp., Alaska to S Argentina, W Indies (some) *Cyclosa*
— Cephalic region with swellings or whole carapace swollen (Figs. 50, 53, 54); abdomen never extending far posteriorly beyond spinnerets 31
31(30) Carapace with a pair of bulges (Figs. 50, 53, 54) 32
— Carapace domed 34
32(31) Abdomen with dorsal, round, sclerotized discs and small spines (Fig. 50); max. 13 mm; 5 sp., Mexico to S Brazil, Jamaica *Xylethrus*
— Abdomen with tubercles and bulges (Figs. 53, 86) 33
33(32) PME facing dorsolaterally (Figs. 53, 54); abdomen with anterior median swelling (Fig. 53); max. 16 mm; 3 sp., Baja California to N Argentina, Jamaica *Carepalxis*
— PME facing dorsally (Fig. 86); abdomen without anterior median swelling (Fig. 86); max. 27 mm; 27 sp, Baja California to Argentina, W Indies (a few) *Parawixia*
34(18, 31) Abdomen with more than one pair of humps or tubercles; with extra tubercles, spines, sclerites or elongated posteriorly (Figs. 43, 48, 51, 55, 56, 63) 35
— Abdomen spherical, oval, sometimes wider than long, with at most one pair of humps or tubercles (Figs. 91, 96, 100, 111, 115, 119), and rarely a median anterior hump or median posterior one (Figs. 112, 131) 55
35(34) Abdomen with asymmetrical tubercles often on symmetrical protrusions, light colored (Figs. 8, 9) and distal articles of first to third legs with dense line of setae and macrosetae (Fig. 8, 9); max. 14 mm; 14 sp., E U. S. to N Argentina, W Indies ..
..... (most) *Kaira*
— All tubercles symmetrical, and legs without dense setae (Figs. 55) 36
36(35) Abdomen wider than long, rectangular, with three to six pairs of pointed, sometimes

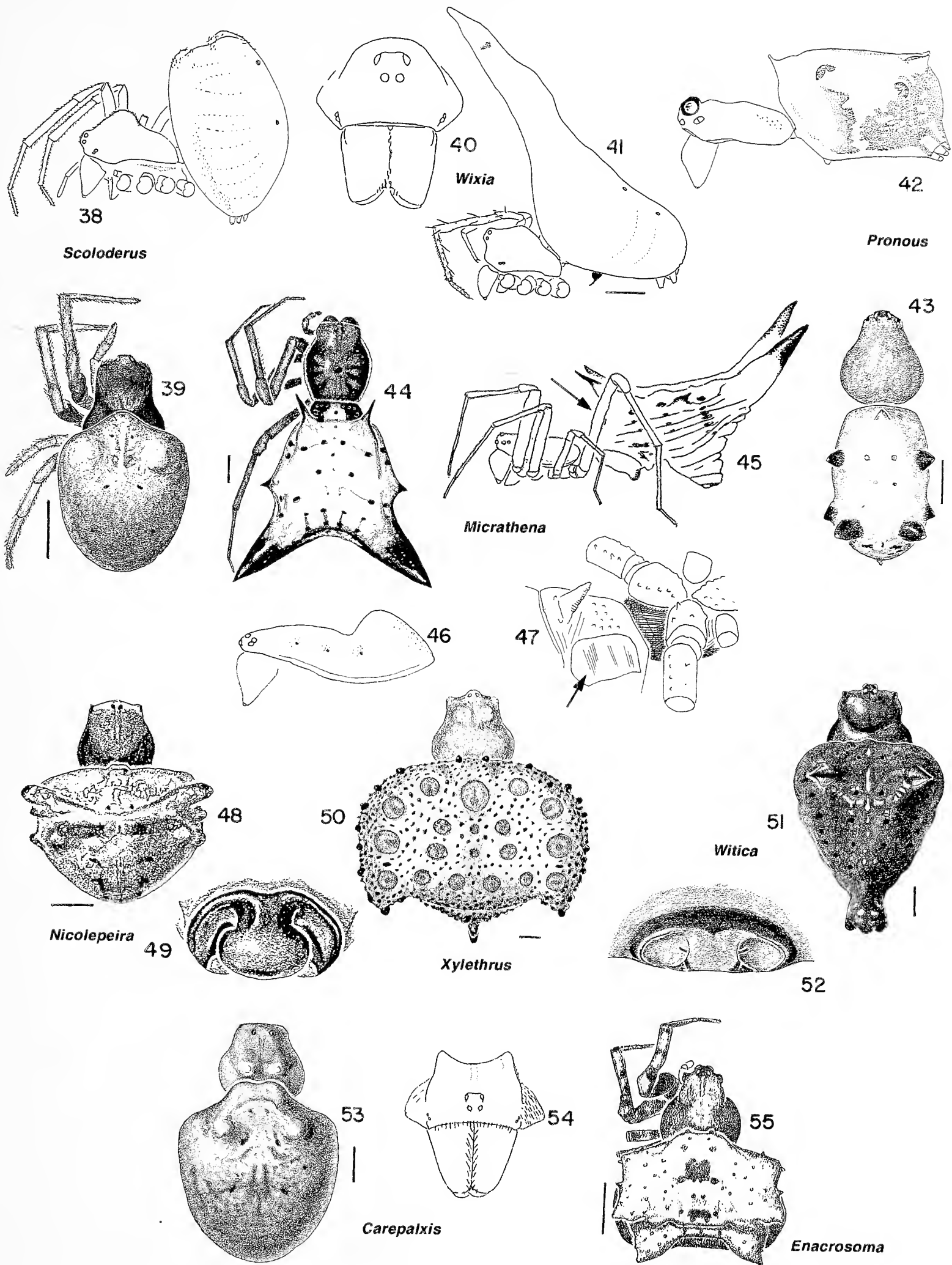


Figures 19–37.—Females: 19. *Spilasma duodecimguttata* (Keyserling 1880), dorsal. 20, 21. *Taczanowskia sextuberculata* (Keyserling 1892). 20. Leg claws; 21. dorsal. 22, 23. *Pozonia nigroventris* (Bryant 1936). 22. Carapace; 23. Lateral. 24. *Acacesia hamata* (Hentz 1847), dorsal. 25. *Mastophora leucacantha* (Simon 1895), carapace, lateral (after Simon). 26, 27. *M. gasteracanthoides* (Nicolet 1849). 26. Dorsal; 27. Carapace and chelicera, lateral. 28. *Testudinaria* sp., dorsal. 29. *Hypognatha mozamba* Levi 1996, sternum. 30. *H. cryptocephala* Mello-Leitão 1947, dorsal. 31. *Encyosaccus sexmaculatus* Simon 1895, dorsal. 32. *Chaetacis cornuta* (Taczanowski 1873), dorsal. 33, 34. *Gasteracantha cancriformis* (Linné 1767). 33, Lateral; 34, Dorsal. 35. *Edricus productus* O. P. -Cambridge 1890, dorsal. 36, 37. *Aspidolasius branicki* (Taczanowski 1879). 36. Carapace and chelicera, lateral; 37. Dorsal. Scale lines = 1mm.

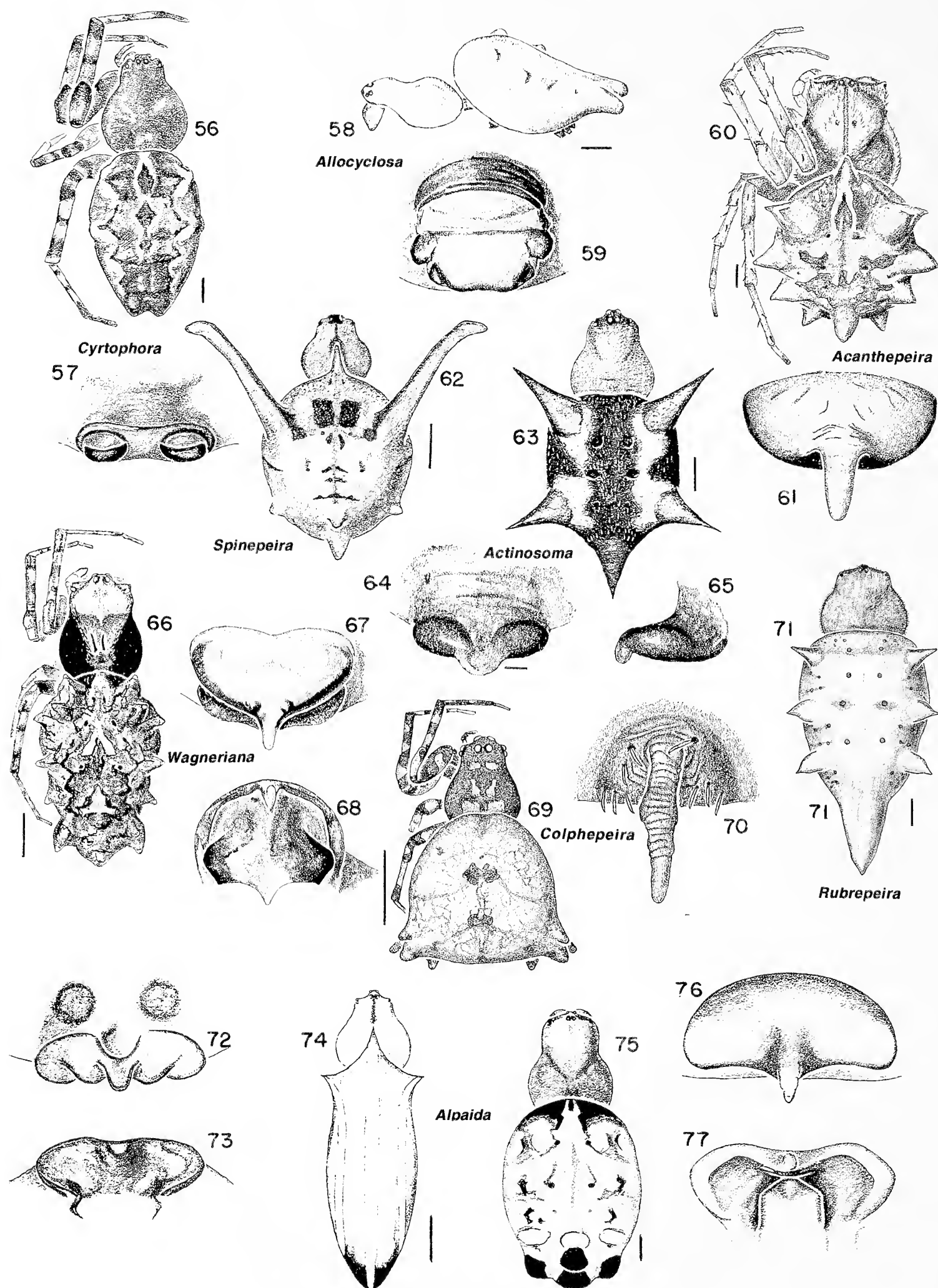
	bulging, tubercles (Fig. 55); max. 5 mm; 6 sp., Mexico to São Paulo State, Brazil	
	<i>Enacrosoma</i>
—	Abdomen longer than wide; trapezoidal if wider than long	37
37(36)	Abdomen dorsally with tortoise sclerites (Fig. 28); max. 4 mm; 9 sp.; Panama to N Argentina	(in part) <i>Testudinaria</i>
—	Abdomen otherwise	38
38(37)	Fourth femur longer than first (Fig. 45)	39
—	Fourth femur subequal or shorter than first	41
39(38)	Venter of abdomen with large, median bulge (Fig. 33), abdomen wider than long, with two or three pairs of large spines (Fig. 34); max. 8 mm; SE U. S. to Argentina, W Indies	<i>Gasteracantha cancriformis</i>
—	Abdomen without ventral bulge	40
40(39)	PME diameter 2–3 times that of AME, black ringed (Figs. 42, 43) and abdomen longer than wide, orange with black patches on 3 pairs of tubercles (Fig. 43); web above leaf litter; max. 5 mm; 14 sp., Mexico to N Argentina	<i>Pronous</i>
—	PME only slightly larger than others, abdomen with paired, pointed spines (Figs. 44, 45); booklung covers usually with microscopic stridulating grooves (Fig. 47); carapace often with pairs of dimples, light thoracic rim, or domed (Fig. 46); max. 13 mm; 104 sp., S Canada to Argentina, W Indies	(in part) <i>Micrathena</i>
41(38)	Epigynum flat, without scape or projecting ridge or lobe (Figs. 49, 52, 57, 59)	42
—	Epigynum with scape (Figs. 61, 70), projecting ridge or lobe (Figs. 64, 76)	45
42(41)	Chile (Fig. 48); max. 7 mm; 3 sp.	(in part) <i>Nicolepeira</i>
—	Subtropical, tropical America	43
43(42)	Posterior of abdomen with a neck and four-knobbed tail (Fig. 51); max. 12 mm; 2 sp., Mexico to Guyanas, Peru, W Indies	<i>Witica</i>
—	Abdomen with dorsal tubercles and posterior notch; social (Figs. 56, 58)	44
44(43)	LE separated (Fig. 56); 10 to 12 mm; introduced	<i>Cyrtophora citricola</i>
—	LE touching (Fig. 58); max. 9 mm, Florida, Baja California to Panama, W Indies	<i>Allocyclosa bifurca</i>
45(41)	Abdomen with anterior, median, usually spine-shaped, tubercle (Figs. 60, 62)	46
—	Abdomen without anterior median projecting tubercle (Figs. 63, 71)	47
46(45)	Abdomen surrounded by about 15 tubercles (Fig. 60); max. 16 mm; 4 sp., Canada to C America, W Indies	<i>Acanthepeira</i>
—	Abdomen with a pair of long, dorsal projections, longer than abdomen, and anterior and posterior median tubercles (Fig. 62); max. 6 mm; Amazonian Peru	<i>Spinepeira schlingeri</i>
47(45)	Epigynum with a transverse ridge, often with a posterior, median, lobe (Figs. 64, 65, 67, 68, 72, 73, 76, 77)	48
—	Epigynum with scape (Figs. 70, 83, 84, 87, 89, 113, 116)	52
48(47)	Abdomen with five large spines (Fig. 63); web above water; max. 10 mm; Ecuador, Amazon area to Argentina	<i>Actinosoma pentacanthum</i>
—	Abdomen otherwise (Figs. 66, 71, 74, 75, 119)	49
49(48)	Abdomen flat, with three pairs of pointed tubercles, and elongated beyond spinnerets (Fig. 71); max. 20 mm; 1 sp., Venezuela, Ecuador to Espírito Santa, Brazil	<i>Rubrepeira rubronigra</i>
—	Abdomen otherwise (Figs. 66, 74, 75, 119)	50
50(49)	Carapace and abdomen glossy; black oval rings on median side of PME (Figs. 74, 75); abdomen basically oval, brightly colored, glabrous (Figs. 74, 75), with paired	

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Figures 38–55.—Females: 38, 39. *Scoloderus nigriceps* O. P.-Cambridge 1895. 38. Lateral; 39 Dorsal. 40, 41. *Wixia abdominalis* O. P.-Cambridge 1882. 40. Eyes, clypeus and chelicerae; 41. Lateral. 42. *Pronous wixoides* (Chamberlin and Ivie 1936), lateral. 43. *Pronous intus* Levi 1995, dorsal. 44, 45. *Mi-*



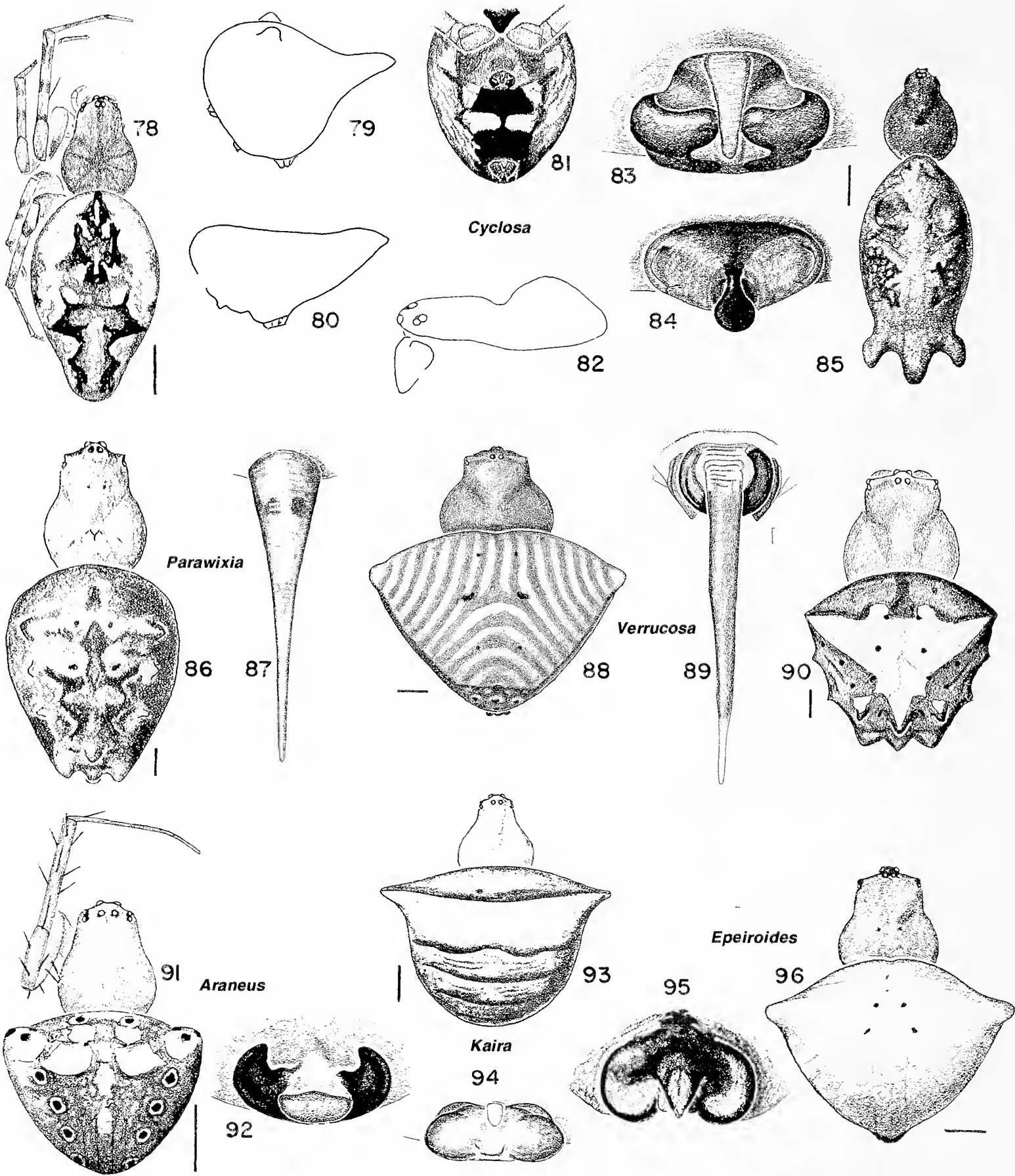
crathena sagittata (Walckenaer 1841). 44. Dorsal; 45. Lateral. 46. *Micrathena* sp., carapace and chelicera. 47. *Chaetacis aureola* (C. L. Koch 1836), booklung cover, epigynum and third and fourth coxae, subventral. 48, 49. *Nicolepeira flavifrons* (Nicolet 1849). 48. Dorsal; 49. Epigynum. 50. *Xylethrus superbis* Simon. 1895, Dorsal. 51, 52. *Witica crassicauda* (Keyserling 1865). 51. Dorsal; 52. Epigynum. 53, 54. *Carepalxis salobrensis* Simon 1895. 53. Dorsal; 54. Eyes, clypeus and chelicerae. 55. *Enacrosoma anomalum* (Taczanowski 1873), dorsal. Scale lines = 1 mm.



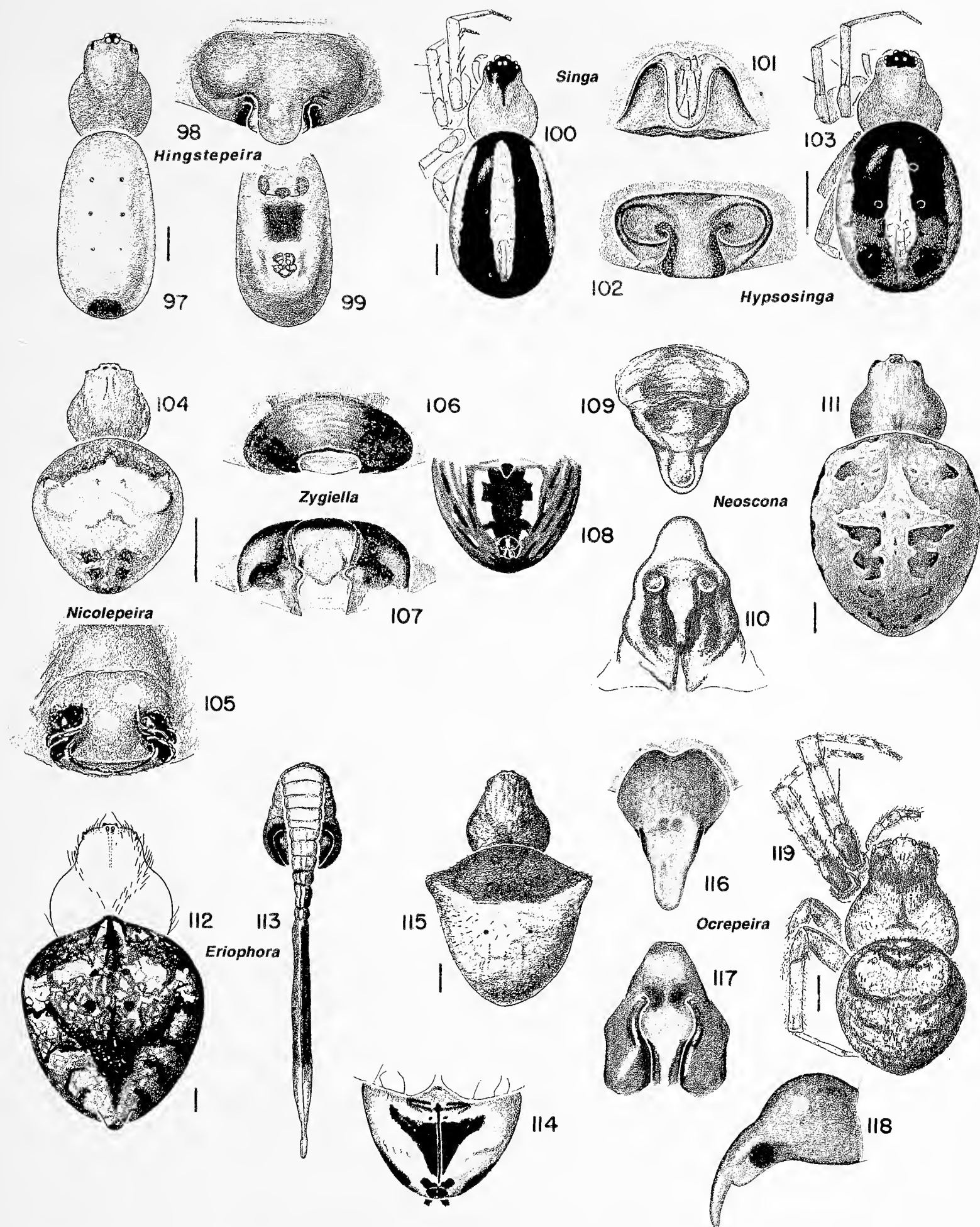
Figures 56–77.—Females: 56, 57. *Cyrtophora citricola* (Forskål 1775). 56. Dorsal; 57. Epigynum. 58, 59. *Allocyclosa bifurca* (McCook 1887). 58. Sublateral; 59. Epigynum. 60, 61. *Acanthepeira stellata* (Walckenaer 1805). 60. Dorsal. 61. Epigynum. 62. *Spinepeira schlingeri* Levi 1955, dorsal. 63–65. *Actinosoma pentacanthum* (Holmberg 1883). 63. Dorsal; 64, 65. Epigynum; 64. Ventral; 65. Lateral. 66. *Wagneriana*, composite, dorsal. 67, 68. *W. maseta* Levi 1991. 67, 68. Epigynum; 67. Ventral; 68. Posterior. 69, 70. *Colphepeira catawba* (Banks 1911). 69. Dorsal; 70. Epigynum. 71. *Rubrepeira rubronigra* (Mello-

	anterior spines or lateral lobes, max. 18 mm; 134 sp., S Mexico to Argentina, W. Indies	(in part) <i>Alpaida</i>	
—	Carapace and abdomen setose		51
51(50)	Abdomen rounded posteriorly (Fig. 119); max. 12 mm; 67 sp., E U. S. to Chile, W. Indies	(a few) <i>Ocrepeira</i>	
—	Abdomen with posterior median tubercle(s) (Fig. 66); abdomen longer than wide, rectangular, with 4–6 pairs of lateral tubercles, cephalic region pale, thorax dark (Fig. 66); max. 16 mm; 39 sp., SE U. S. to Argentina, W Indies	(in part) <i>Wagneriana</i>	
52(47)	Abdomen longer than wide, pointed, elongated beyond spinnerets (Figs. 79, 80) and scape not extending far, if at all, beyond base of epigynum (Figs. 83, 84); orb decorated with line of debris; max. 12 mm; 51 sp., Alaska to S Argentina, W Indies	(in part) <i>Cyclosa</i>	
—	Abdomen without pointed, posterior tail (Figs. 69, 86, 88, 90) and usually scape greatly extended posteriorly beyond base (Figs. 70, 87, 89)		53
53(52)	Four tubercles on each of a pair of posterior bulges on subspherical abdomen (Fig. 69); web on base of trees; max. 4 mm; SE U. S.	<i>Colphepeira catawba</i>	
—	Abdomen otherwise (Figs. 86, 88, 90); total length usually more than 5 mm . . .		54
54(53)	Carapace, abdomen glossy; abdomen trapezoidal, narrowest behind (Figs. 88, 90), black-topped tubercles posteriorly and on sides (Figs. 88, 90); max. ca. 15 mm; ca. 15 sp., E U. S. to Argentina, W Indies	(most) <i>Verrucosa</i>	
—	Carapace, abdomen setose; abdomen longer than wide, round to trapezoidal with two to six pairs of brown tubercles on sides and posterior median tubercles (Fig. 86); max. 27 mm; 26 sp., Baja California to Argentina, W Indies . .	(most) <i>Parawixia</i>	
55(34)	Abdomen wider than long (Figs. 88, 91, 93, 96)		56
—	Abdomen as wide as long or longer than wide (Figs. 97, 100, 103, 104, 111) . .		59
56(55)	Scape with distal end rounded and with lip (Fig. 92); ca. 165 sp., Alaska to Chile, W Indies	(a few) <i>Araneus</i>	
—	Scape otherwise (Figs. 89, 94, 95)		57
57(56)	Scape pointed, straight and long (Fig. 89); abdomen glossy, dorsally with pattern of lines (Fig. 88); max. ca. 15 mm; SE Brazil	<i>Verrucosa zebra</i>	
—	Scape short, not extending beyond base (Figs. 94, 95); abdomen with lateral tubercles (Figs. 93, 96)		58
58(57)	Legs with black lines; sclerotized epigynum (Fig. 95), lateral plates surround median plate in posterior view; max. 8 mm; Costa Rica to Bahia, Brazil	<i>Epeiroides bahiensis</i>	
—	Legs without black lines; weakly sclerotized epigynum (Fig. 94), median plate overhangs laterals in posterior view; abdomen with transverse lines (Fig. 93); max. 14 mm; 14 sp., E U. S. to Argentina, W Indies	(a few) <i>Kaira</i>	
59(55)	Abdomen cylindrical, widest in posterior half (Figs. 97, 100)		60
—	Abdomen oval, spherical (Figs. 103, 104, 171)		62
60(59)	Temperate; abdomen dorsally with three white lines separated by two longitudinal black bands; black cephalic region (Fig. 100); max. 11 mm; 2 sp., E Canada, U. S.	<i>Singa</i>	
—	Tropical; abdomen otherwise		61
61(60)	Posterior of abdomen with black patch (Fig. 97) or longitudinal lines; scape spherical or with ridge, max. 8 mm; 4 sp., Guyanas to C Amazon area.	<i>Hingstepeira</i>	

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Leitão 1939), dorsal. 72–74. *Alpaida trispinosa* (Keyserling 1892). 72, 73. Epigynum; 72. Ventral; 73. Posterior. 74. Dorsal. 75–77. *Alpaida truncata* (Keyserling 1865). 75. Dorsal; 76, 77. Epigynum; 76. Ventral; 77. Posterior. Scale lines = 1 mm.

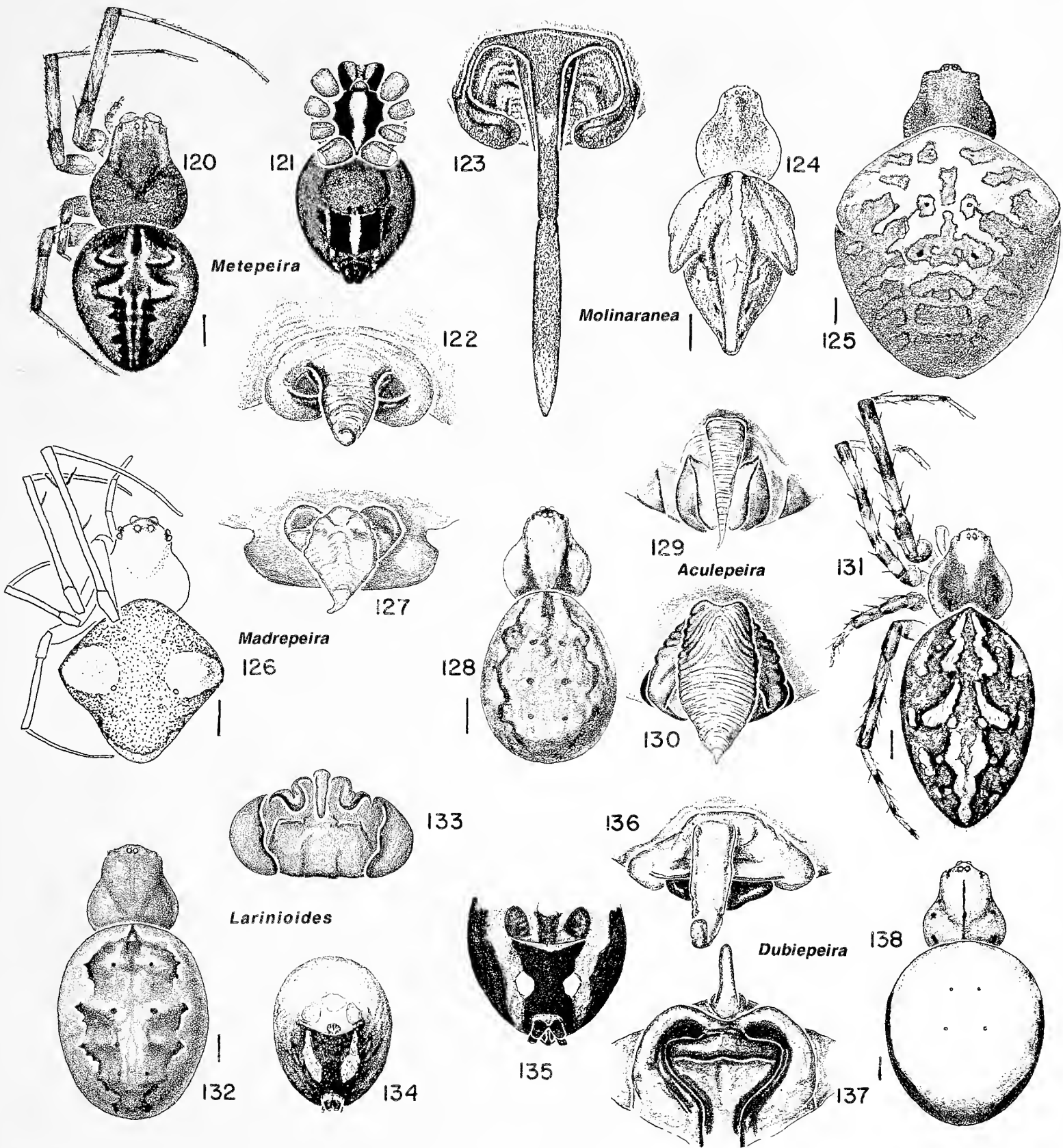


Figures 78–96.—Females: 78, 81, 83. *Cyclosa conica* (Pallas 1772). 78. Dorsal; 81. Abdomen, ventral; 83. Epigynum.. 79. *C. monteverde* Levi 1999, abdomen, lateral. 80. *C. pedropalo* Levi 1999, abdomen, lateral. 82. *Cyclosa* sp., carapace and chelicera, lateral. 84, 85. *Cyclosa bifurcata* (Keyserling 1841). 84. Epigynum; 85. Dorsal. 86, 87. *Parawixia kochi* (Taczanowski 1873). 86. Dorsal; 87. Epigynum. 88. *Verrucosa zebra* (Keyserling 1892), Dorsal. 89, 90. *V. arenata* (Walckenaer 1841). 89. Epigynum; 90. Dorsal. 91, 92. *Araneus partitus* (Walckenaer 1841). 91. Dorsal; 92. Epigynum. 93, 94. *Kaira sexta* (Chamberlin 1916). 93. Dorsal; 94. Epigynum. 95, 96. *Epeiroides bahiensis* Keyserling 1885. 95. Epigynum, 96. Dorsal. Scale lines = 1 mm.



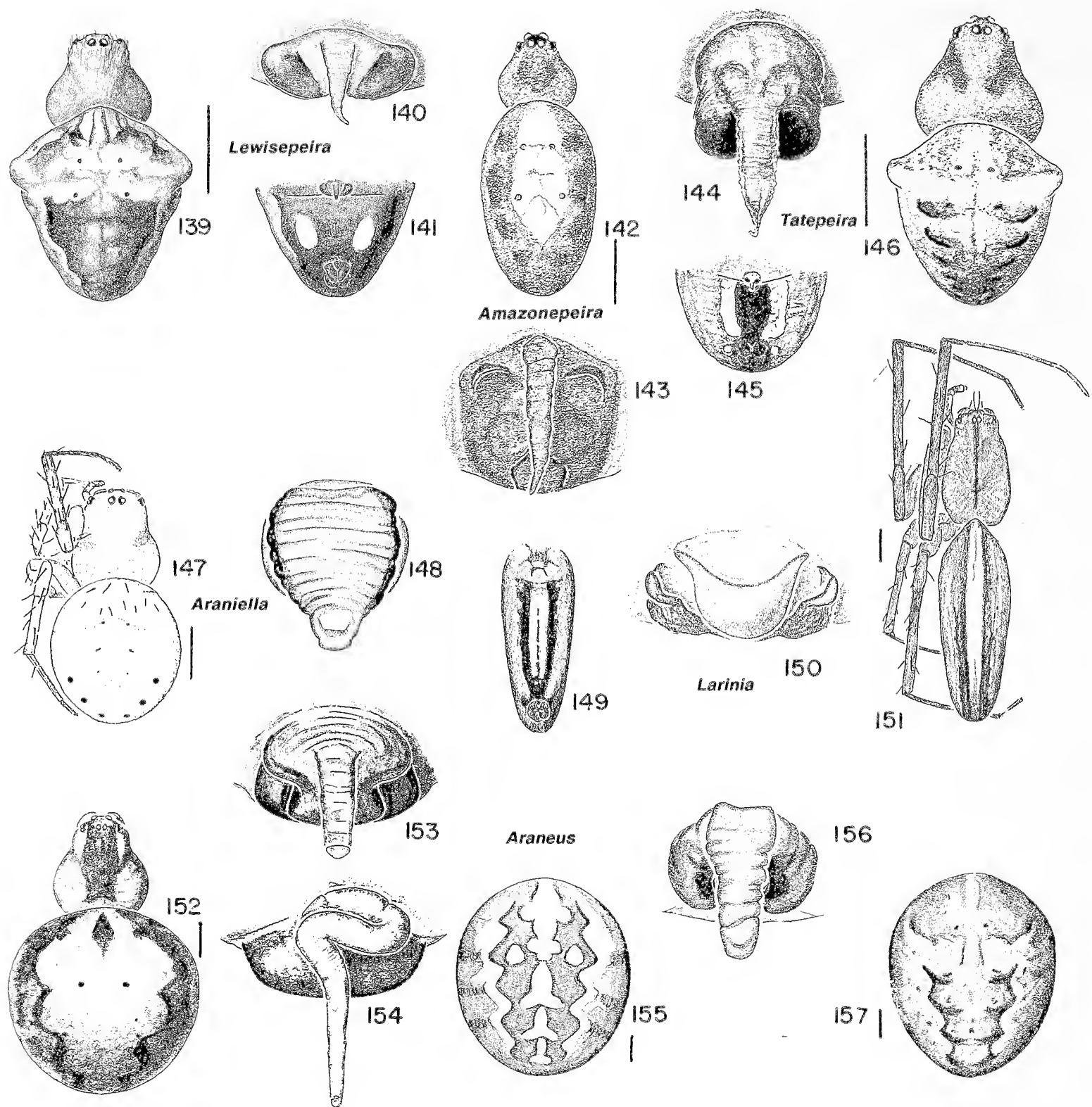
Figures 97–118.—Females. 97–99. *Hingstepeira folisecens* (Hingston 1932). 97. Dorsal; 98. Epigynum; 99. Abdomen, ventral. 100–101. *Singa keyserlingi* McCook 1893. 100. Dorsal; 101. Epigynum. 102. 103. *Hypsosinga pygmaea* (Sundeval 1831). 102. Epigynum, 103. Dorsal. 104, 105. *Nicolepeira transversalis* (Nicolet 1849). 104. Dorsal; 105. Epigynum. 106, 107. *Zygiella dispar* (Kulczynski 1885), epigynum. 106. Ventral; 107. Dorsal.. 108–111. *Neoscona nautica* (L. Koch 1875). 108. Abdomen, ventral; 109, 110. Epigynum; 109. Ventral; 110. Posterior; 111. Dorsal. 112, 113. *Eriophora edax* (Blackwall 1863). 112. Dorsal; 113. Epigynum. 114. *E. fuliginea* (C.L. Koch 1843), abdomen, ventral. 115. *Ocrepeira subrufa* (F. P. -Cambridge 1904), dorsal. 116–118. *O. lurida* (Mello-Leitão 1943), epigynum. 116. Ventral; 117. Posterior; 118. Lateral.. 119. *O. georgia* (Levi 1976), dorsal. Scale lines = 1 mm.

—	Abdomen with folium (Fig. 158); epigynum otherwise; max. 11 mm; Mexico to Bolivia	(most) <i>Metazygia</i>
62(59)	Epigynum flat, with depressions (Figs. 102, 105–107)	63
—	Epigynum with scape, projecting lobe or ridge (Figs. 113, 116, 123, 159, 168–170), (rarely scape or lobe is torn off)	66
63(62)	Chile; abdomen with humps, as long as wide (Fig. 104); max. 6 mm.	<i>Nicolepeira transversalis</i>
—	Tropical or nearctic; abdomen without humps (Figs. 28, 103, 171)	64
64(63)	Tropical, abdomen flattened, shield shaped (Fig. 28); max. 4 mm; 9 sp.; Panama to N Argentina	(in part) <i>Testudinaria</i>
—	Nearctic, abdomen oval	65
65(64)	Epigynum usually with septum (Fig. 102); median eye region black; abdomen usually dark, dorsally with black folium or bands (Fig. 103); max. 5 mm; 5 sp., Alaska to S U. S.	<i>Hypsosinga</i>
—	Epigynum without septum; eye region light or in gray carapace band, abdomen light with folium (Fig. 171); max. 9 mm; 5 sp., Alaska to U. S.	(in part) <i>Zygiella</i>
66(62)	Epigynum with scape, often with annuli, usually annulated if shorter than wide (Figs. 109, 113, 116, 122, 123)	67
—	Epigynum with lobe or projecting ridge or keel, without annuli (Figs. 159–161, 165, 166, 168–170, 172–174)	86
67(66)	Base of epigynum indistinct, tapering into a smooth scape (Figs. 109, 113, 116–118)	68
—	Base distinct, scape set off from base (Figs. 122, 123, 129, 136)	72
68(67)	Scape of epigynum projecting anteriorly, turned back on itself; base is first annulus of scape or is minute (Fig. 113); venter of spherical abdomen with discrete, trapezoidal to triangular black patch (Fig. 114); max. 30 mm; 4 sp., S U. S. to Rio de Janeiro State, Brazil	(in part) <i>Eriophora</i>
—	Scape not turned on itself (Figs. 109, 110, 116–118)	69
69(68)	Scape smooth, rounded, usually with lip (Figs. 109, 110); max. 20 mm; 10 sp., Canada to Argentina, W Indies	<i>Neoscona</i>
—	Scape otherwise	70
70(69)	PME facing dorsolaterally (Figs. 24, 115, 119)	71
—	PME face dorsally; scape long, annulated, pointed (Fig. 87); abdomen spherical; larger than 15 mm, max. 27 mm; social; cerrado savanna of Brazil, Paraguay, Argentina	<i>Parawixia bistriata</i>
71(70)	Abdomen without humps, light colored with distinct pattern of two parallel lines and an outer pair forming a diamond (Fig. 24), attached at anterior end; max. 9 mm; 8 sp., E U. S. to N Argentina, W Indies	(in part) <i>Acacesia</i>
—	Abdomen with distinct humps and attached near its middle (Fig. 115, 119); max. 12 mm; 67 sp., E U. S. to Chile, W Indies	(in part) <i>Ocrepeira</i>
72(67)	Base with a depression on each side of scape (Fig. 123), scape usually extends beyond base by a distance of width of base or more (Fig. 123), venter of abdomen with paired white spots or longitudinal lines; max. 18 mm; 7 sp.; Chile, Argentina	(in part) <i>Molinaranea</i>
—	Base without depressions, scape not as long (Figs. 122, 129, 133, 136) or if with depressions not found in Chile, Argentina but in tropics	73
73(72)	Tip of scape pointed (Figs. 122, 127, 129, 133, 140, 144), rarely with a knob at distal end of scape	74
—	Tip of scape rounded (Figs. 148, 150, 153, 156)	84
74(73)	Abdomen oval with ventral, median, longitudinal, white line (Fig. 121) and dorsal folium (Fig. 120); tarsi and metatarsi longer than patellae and tibiae (Fig. 120); epigynum with scape barely extending beyond base (Fig. 122); many social; max. 12 mm; 41 sp., U. S. to S. Chile, W Indies	<i>Metepeira</i>
—	Abdomen, if with ventral white line, with dorsal folium as in Figs. 128, 131	75



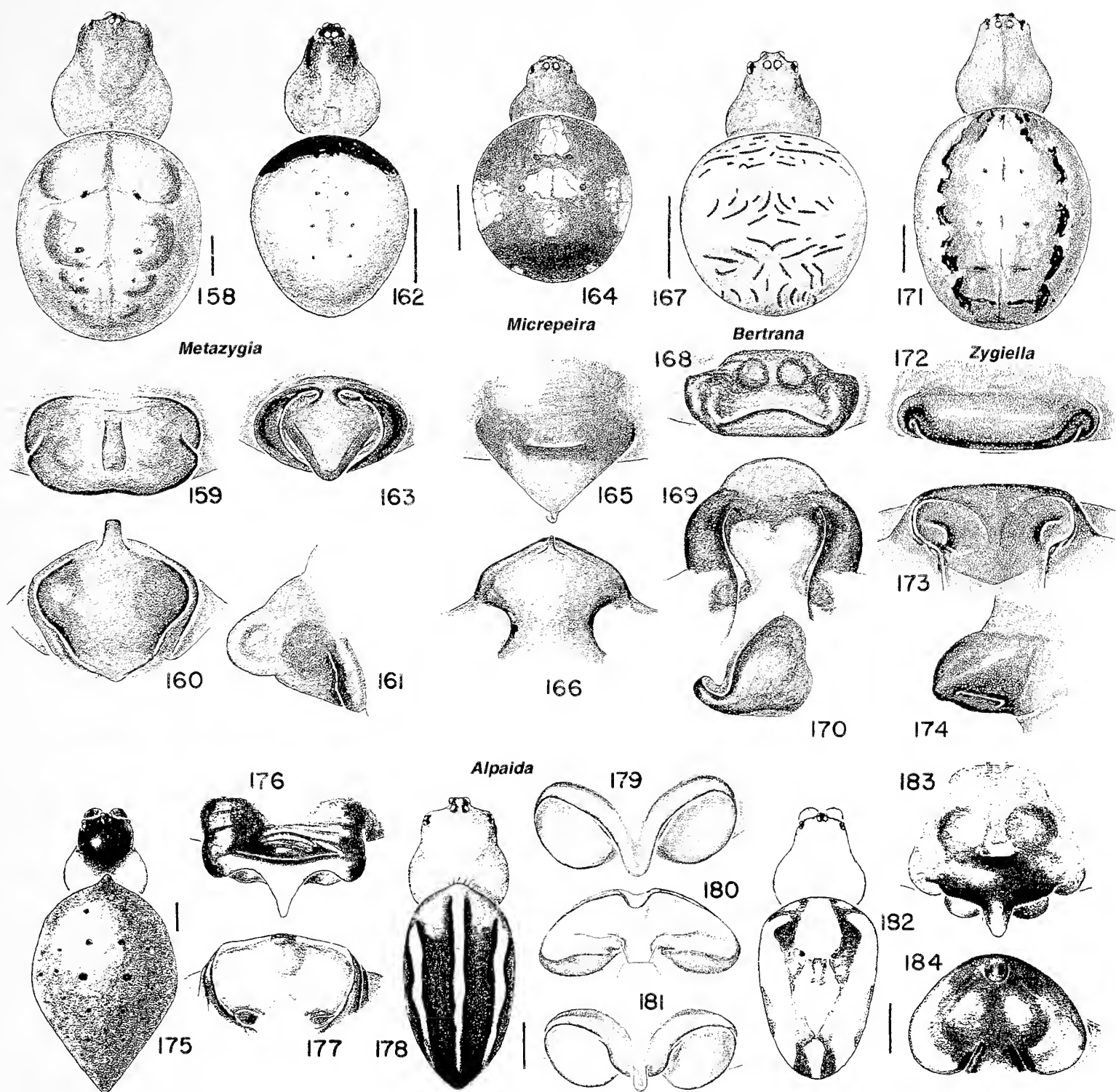
Figures 120–138.—Females: 120–122. *Metepeira labyrinthea* (Hentz 1847). 120. Dorsal; 121. Ventral; 122. Epigynum.. 123, 125. *Molinaranea magellanica* (Walckenaer 1847). 123. Epigynum; 125. Dorsal. 124. *Molinaranea phaethontis* (Simon 1896), dorsal. 126, 127. *Madrepeira amazonica* Levi 1995. 126. Dorsal; 127. Epigynum. 128, 129. *Aculepeira travassosi* (Soares & Camargo 1948). 128. Dorsal; 129. Epigynum. 130, 131. *A. packardi* (Thorell 1875). 130. Epigynum. 131, Dorsal. 132–134. *Larinioides cornutus* (Clerck 1757). 132. Dorsal; 133. Epigynum; 134. Abdomen, ventral. 135–138. *Dubiepeira dubitata* (Soares & Camargo 1948). 135. Abdomen, ventral; 136, 137. Epigynum; 136. Ventral; 137. Posterior; 138. Dorsal. Scale lines = 1 mm.

75(74)	Nearctic	76
—	Neotropical	77
76(75)	Abdomen oval, dorsoventrally flattened (Fig. 132), venter with pair of white comma-shaped patches (Fig. 134); scape sometimes tipped by flat knob (Fig. 133); max. 14 mm; 3 sp., Alaska to U. S.	<i>Larinioides</i>



Figures 139–157.—Females: 139–141. *Lewisipeira farri* (Archer 1958). 139. Dorsal; 140. Epigynum; 141. Abdomen, ventral. 142, 143. *Amazonepeira beno* Levi, 1994. 142. Dorsal; 143. Epigynum.. 144–146. *Tatepeira tatarendensis* (Tullgren 1905); 144. Epigynum; 145. Abdomen, ventral; 146. Dorsal. 147, 148. *Araniella displicata* (Hentz 1847). 147. Dorsal; 148. Epigynum. 149–151, *Larinia directa* (Hentz 1847). 149. Abdomen, ventral; 150. Epigynum; 151. Dorsal. 152, 153. *Araneus corporosus* (Keyserling 1892). 152. Dorsal; 153. Epigynum. 154. *Araneus guttatus* (Keyserling 1865), epigynum. 155. *Araneus marmoreus* (Clerck 1757), abdomen, dorsal. 156, 157. *Araneus nordmanni* (Thorell 1870). 156. Epigynum; 157, Abdomen, dorsal. Scale lines = 1mm.

- Abdomen (Fig. 131) elongate, venter with median white line; max. 17 mm; 13 sp., Alaska to Mexico (in part) *Aculepeira*
- 77(75) Abdomen diamond-shaped, with two light patches; legs spindly (Fig. 126); max. 6 mm; Amazon to Bolivia, Bahia, Brazil *Madrepeira amazonica*
- Abdomen triangular to round (Fig. 138), legs normal thickness 78
- 78(77) Abdomen subtriangular, almost as wide as long and PME facing forward (Fig. 139); pair of ventral white spots (Fig. 141); scape extending posteriorly a distance less



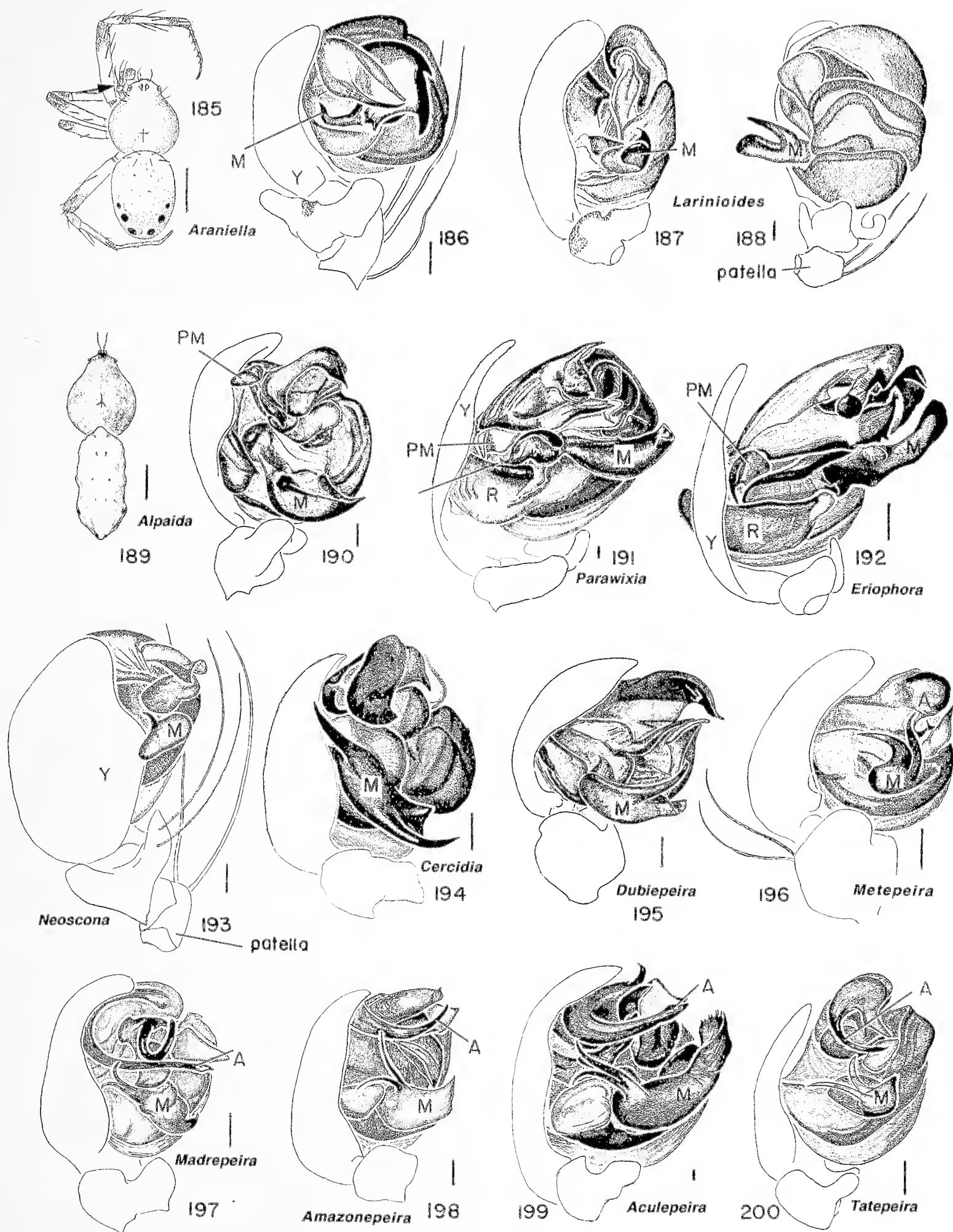
Figures 158–184.—Females: 158–161. *Metazygia wittfeldae* (McCook 1894). 158. Dorsal; 159–161. Epigynum; 159. Ventral; 160. Posterior; 161. Lateral. 162. 163. *M. genaro* Levi 1995. 162. Dorsal; 163. Epigynum. 164–166. *Micrepeira fowleri* Levi 1995. 164. Dorsal; 165, 166. Epigynum; 165. Ventral; 166. Posterior. 167–170. *Bertrana striolata* Keyserling 1884. 167, Dorsal; 168–170. Epigynum; 168. Ventral; 169. Posterior; 170. Lateral. 171–174. *Zygiella x-notata* (Clerck 1757). 171. Dorsal; 172–174. Epigynum; 172. Ventral; 173. Posterior; 174. Lateral. 175–177. *Alpaida acuta* (Keyserling 1865). 175. Dorsal; 176, 177. Epigynum; 176. Ventral; 177. Posterior. 178–181. *A. leucogramma* (White 1841). 178. Dorsal; 179–181. Epigynum. 179. Ventral; 180. Posterior; 181. Ventral. 182–184. *A. championi* (O. P.-Cambridge 1889). 182. Dorsal; 183, 184. Epigynum; 183. Ventral; 184. Posterior. Scale lines = 1mm.

- than base length (Fig. 140) max.; 7 mm; 4 sp., Mexico, C America, W Indies *Lewisipeira*
- Abdomen otherwise; PME facing dorsally 79
- 79(78) Scape of epigynum twisted at proximal end (Fig. 154); max 16 mm; ca 4 sp.; tropical (in part) *Araneus*
- Scape of epigynum straight 80
- 80(79) Venter of base of epigynum soft (Fig. 136), posterior sclerotized (Fig. 137); abdomen oval, no humps, with discrete, black marks (Figs. 135, 138); max. 15 mm; 5 sp., Guyanas to N Argentina *Dubiepeira*

—	Venter and posterior of epigynum sclerotized (Figs. 83, 84, 144)	81
81(80)	Abdomen spherical to elongate (Figs. 79, 80); carapace light; PME adjacent (Fig. 78); orb decorated with line of debris; max. 5mm; 51 sp., Amazon	
— (a few sp.) <i>Cyclosa</i>	
—	Abdomen otherwise; PME separated by about their diameter	82
82(81)	Abdomen narrow, length one and three-quarters its width (Fig. 142); eye area often black (Fig. 142); base of epigynum flat with little sculpturing (Fig. 143); max. 5 mm; 5 sp., Amazon area	
— <i>Amazonepeira</i>	
—	Abdomen wider, eye region light (Figs. 128, 146) and base of epigynum sculptured (Figs. 129, 144)	83
83(82)	Abdomen oval in outline, slightly flattened, sometimes with slight humps (Fig. 128); epigynum (Fig. 129); max. 17 mm; 13 sp., South America	
— (in part) <i>Aculepeira</i>	
—	Abdomen with distinct dorsal or lateral humps (Fig. 146); max. 14 mm; 4 sp., Honduras to S Brazil	
84(73) <i>Tatepeira</i>	
—	Two or three pairs of round black spots dorsally on posterior of round yellow to green abdomen (Fig. 147); max. 8 mm; 2 sp., Alaska to S U. S.	
— <i>Araniella</i>	
—	Abdomen without pairs of black, round spots (Figs. 151, 152, 155, 157)	85
85(84)	Abdomen elongate, often with anterior median hump (Fig. 151), venter with median, white streak (Fig. 149); max. 12 mm; 11 sp., S Canada to Argentina, W Indies	
— <i>Larinia</i>	
—	Abdomen spherical or oval (Figs. 152, 155, 157), without median hump, and without ventral white streak; max. 28 mm; ca. 165 sp., Alaska to Chile, W Indies	
86(66) (most) <i>Araneus</i>	
—	PME almost touching (Figs. 158, 162); carapace glossy; max. 12 mm; 88 sp., S U. S. to Argentina	
— (most) <i>Metazygia</i>	
—	PME more than one-half their diameter apart (Figs. 164, 167, 171, 178)	87
87(86)	Epigynal ridge with a minute, transparent scape at its tip (Fig. 165); abdomen spherical with contrasting pattern (Fig. 164); max. 7 mm; 7 sp., Costa Rica to Mato Grosso	
— <i>Micrepeira</i>	
—	Lobe without minute scape on tip (Figs. 168, 172, 176)	88
88(87)	PME facing dorsolaterally (Fig. 119) and abdomen attached one third from its anterior end (Fig. 119); max. 12 mm; 67 sp., E U. S. to Chile, W Indies	
— (a few) <i>Ocrepeira</i>	
—	PME facing dorsally; abdomen attached at its anterior end (Figs. 167, 171, 178)	89
89(88)	Abdomen spherical, as wide as long (Fig. 167); max. 4 mm; 13 sp., Costa Rica to S Brazil	
— <i>Bertrana</i>	
—	Abdomen oval to elongate (Figs. 171, 175, 178, 182)	90
90(89)	Epigynum ridge usually with secondary median, smaller lobe on its edge (Figs. 176, 177, 179–181, 183, 184); carapace yellow, posterior median eyes bordered by black sickle on its mesal side (Figs. 175, 178, 182); body glossy; max. 18 mm; 134 sp., S Mexico to Argentina, W Indies	
— (most) <i>Alpaida</i>	
—	Epigynum ridge without secondary smaller lobe bearing two posterior depressions (Figs. 172–174); max. 8 mm; Alaska to U. S., introduced in Argentina, Chile	
— <i>Zygiella x-notata</i>	

KEYS TO MALES

Males of American *Carepalxis*, *Spinepeira* and *Rubrepeira* are unknown. The male of *Carepalxis* may have a branched second tibia and swellings on the carapace, as do males from Australia. Presumably the male of *Spinepeira* has the posterior median eyes facing sideways.



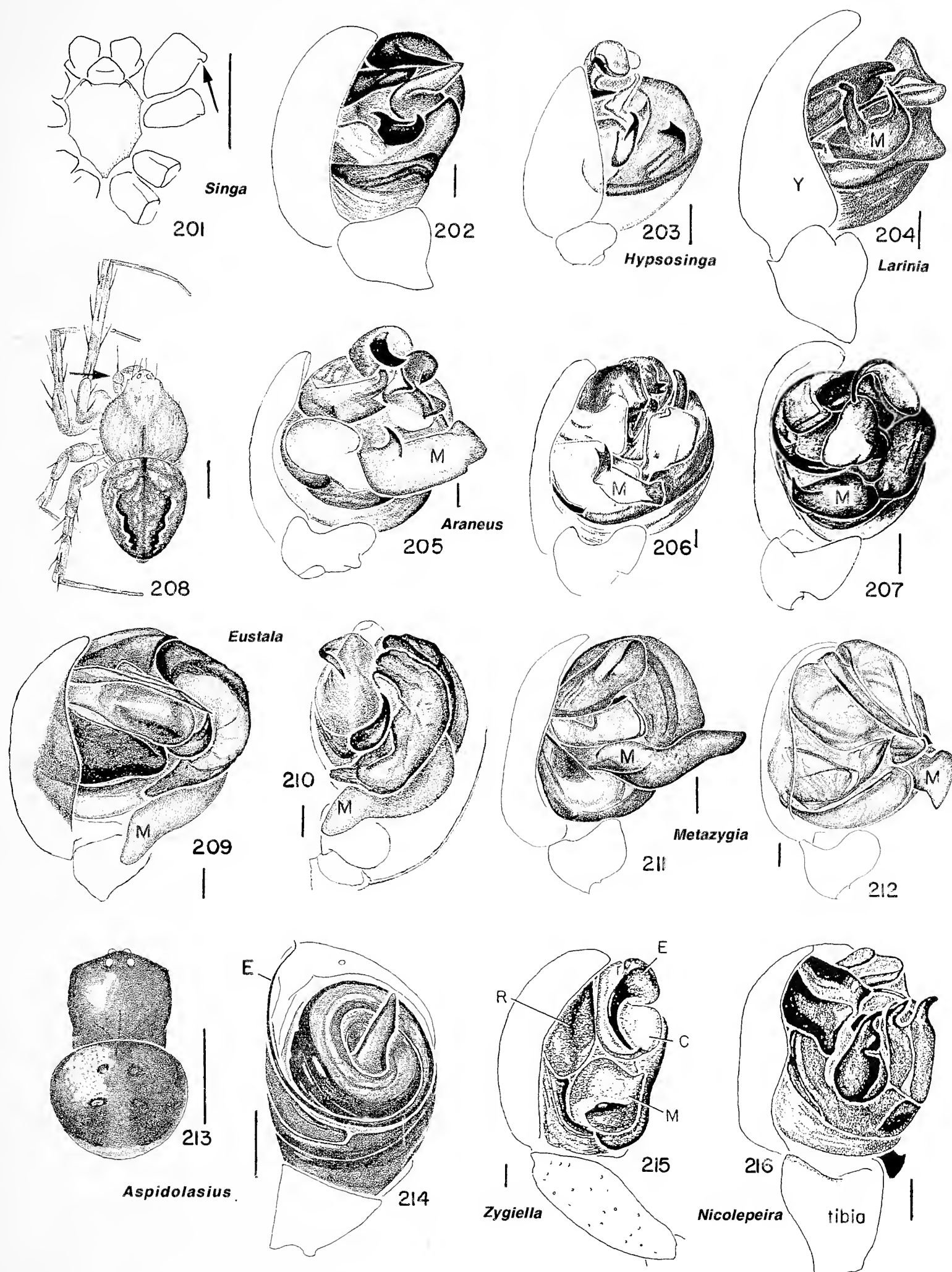
Figures 185–200.—Males: 185, 186. *Araniella displicata* (Hentz 1847). 185. Dorsal; 186. Palpus. 187, 188. *Larinioides cornutus* (Clerck 1757), Palpus; 187. Mesal; 188. Ventral. 189, 190. *Alpaida almada* Levi 1988. 189. Dorsal; 190. Palpus. 191. *Parawixia bistriata* (Rengger 1836), palpus. 192. *Eriophora fuliginea* (C.L. Koch 1843), Palpus. 193. *Neoscona arabesca* (Walckenaer 1841), palpus. 194. *Cercidia prominens* (Westring 1851), palpus. 195. *Dubiepeira dubitata* (Soares & Camargo 1949), palpus. 196. *Metepeira labyrinthea* (Hentz 1847), palpus. 197. *Madrepeira amazonica* Levi 1995, palpus. 198. *Amazonopeira masaka* Levi 1994, palpus. 199. *Aculepeira packardi* (Thorell 1875), palpus. 200. *Tatepeira tatarendensis* (Tullgren 1905), palpus. Scale lines = 1mm; palpi, 0.1 mm.

SPEED KEY FOR MALES

- 1 Palpal patella with two or more long macrosetae (Figs. 185, 188). Go to 1 in key for males, or if not to 19 below.
- 19(1) Third tibia with anterior feathery trichobothria (as in female, Fig. 2). Go to 19 in key, or if not to 20 below.
- 20(19) Median apophysis soft, white, worm-shaped (Fig. 209, 211). Go to 20 in main key, or if not to 22 below.
- 22(20) Palpal tibia cone-shaped, as long or longer than wide (Figs. 214–216). Go to 22 in key, or if not to 25 below.
- 25(22) Carapace with projections (Fig. 217), pairs of dimples (Fig. 224), tubercles (as in female, Figs. 25, 27), bulges (Fig. 231), spines or denticles (Fig. 222), or elongated (Fig. 229). Go to 25 in key, or if not to 34 below.
- 34(25) Posterior row of eyes procurved (Figs. 237, 241). Go to 34 in key, or if not to 38 below.
- 38(34) Abdomen modified with dorsal sclerotized areas (Figs. 225, 226, 245), more than two tubercles (Fig. 251, 253), or elongated (Figs. 263, 264). Go to 38 key, or if not to 56 below.
- 56(38) Abdomen oval with posterior notch (Fig. 275). Go to 56 in key, or if not to 58 below.
- 58(56) Abdomen wider than long (Figs. 277, 279). Go to 58 in key, or if not to 61 below.
- 61(58) Paramedian apophysis present (Fig. 286) or fourth coxae with short macroseta (Figs. 285, 288). Go to 61 in key, or if not to 69 below.
- 69(61) Without PM; fourth coxae never with macroseta. Go to 69 in key.

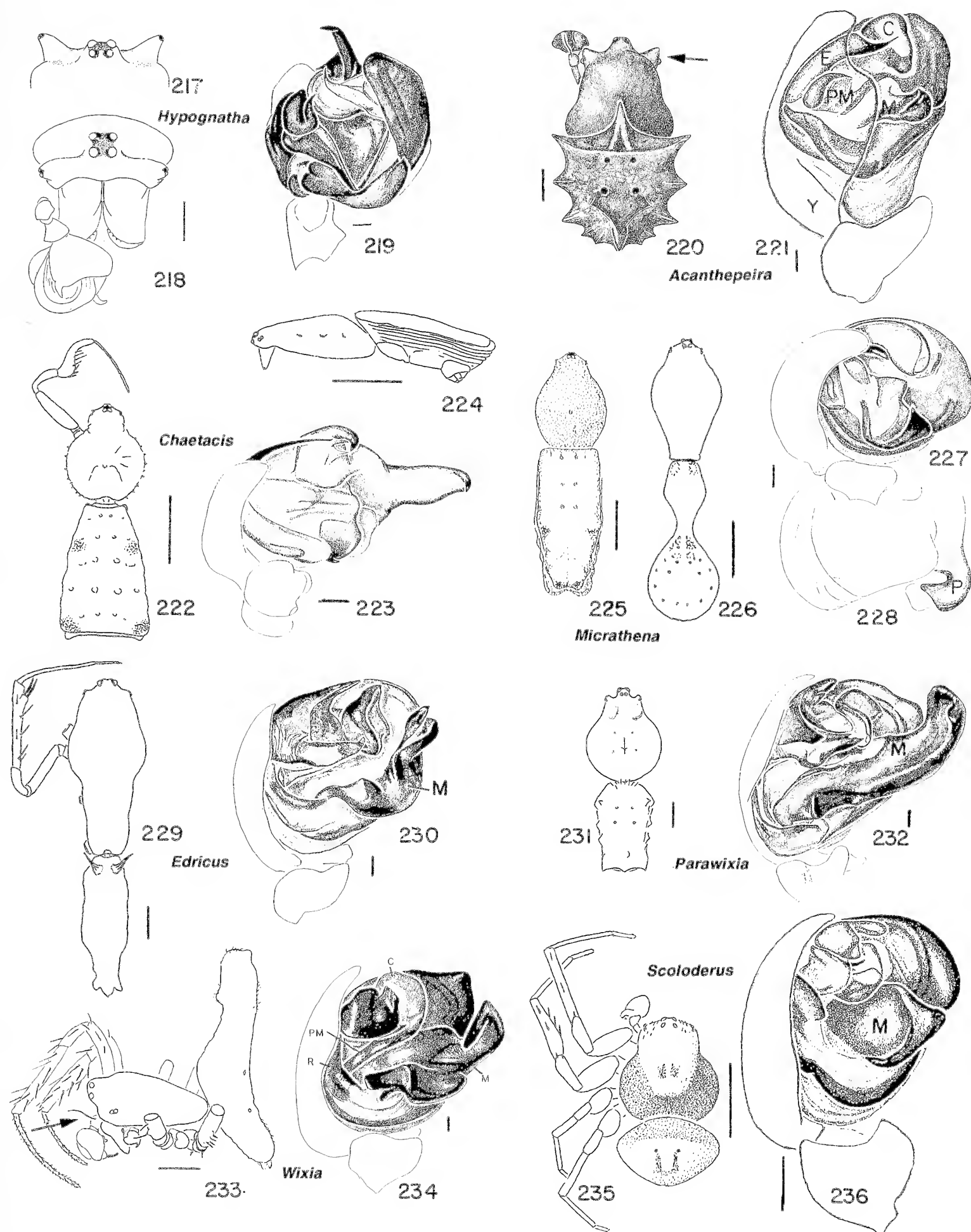
KEY FOR MALES

- 1. Palpal patella with two or more long macrosetae (Figs. 185, 186, 188, 193), one may be stronger than other 2
- Palpal patella with one macroseta or none (Figs. 208, 233) 19
- 2(1) Palpal patella with three or more macrosetae, rarely only two, two distally, one proximally and M pointing toward Y (Fig. 186); abdomen yellow to green with 2 or 3 pairs of round, black spots (Figs. 185); max. 5 mm; 2 sp., Alaska to U. S. *Araniella*
- Palpal patella with two macrosetae (Figs. 188, 193); M and abdomen otherwise 3
- 3(2) M split into two parallel, projecting branches (Figs. 187, 188); abdomen, oval, flattened (as in female, Fig. 132); max. 5 mm; 3 sp.; Alaska to U. S. *Larinioides*
- M otherwise 4
- 4(3) Abdomen with undulating sides (Fig. 189); carapace yellow with black eye region; palpus (Fig. 190); max. 11 mm; Panama to Brazil (a few) *Alpaida*
- Abdomen with sides evenly rounded 5
- 5(4) Prominent PM next to R and Y (Figs. 191, 192); M elongate, without spines (Figs. 191, 192); subtropical 6
- Without PM (Figs. 193–200) 7
- 6(5) Ventral abdominal markings indistinct; proximal end of M with small tooth facing PM (Fig. 191); max. 19 mm; S Brazil, Paraguay, N Argentina *Parawixia bistrata*
- With discrete, trapezoidal black patch on abdomen venter (as in female, Fig. 114); proximal end of M without tooth (Fig. 192); max. 16 mm; 4 sp., S U. S. to Rio de Janeiro State, Brazil, W Indies *Eriophora*
- 7(5) Patellar macrosetae of unequal thickness and M as wide as long, almost round, touching Y (Fig. 304); abdomen spherical, oval (Fig. 303); max. 3 mm; 13 sp., Costa Rica to S Brazil (in part) *Bertrana*
- Patellar macrosetae subequal or N of Costa Rica 8
- 8(7) M in middle of palpus with tooth touching or overhanging Y (Fig. 193); two long patellar setae (Fig. 193); max. 15 mm; 10 sp., Canada to Argentina, W Indies *Neoscona*
- M otherwise, 9
- 9(8) Abdomen orange, with scutum, pointed anteriorly (as in female, Fig. 7); M drawn out



Figures 201–216.—Males: 201, 202. *Singa eugeni* Levi 1972. 201. Sternum and left coxae; 202. Palpus. 203. *Hypsosinga rubens* (Hentz 1847), palpus. 204. *Larinia directa* (Hentz 1847), palpus. 205. *Araneus diadematus* (Clerck 1757), palpus. 206. *A. bogotensis* (Keyserling 1864), palpus. 207. *A. detrimentosus* (O. P.-Cambridge 1889), palpus. 208–210. *Eustala anastera* (Walckenaer 1841); 208, dorsal. 209, 210. Palpus; 209. Mesal; 210. Ventral. 211. *Metazygia nigrocincta* (F. P.-Cambridge 1904), palpus. 212. *M. wittfeldae* (McCook 1894), palpus. 213, 214. *Aspidolasius branicki* (Taczanowski 1879). 213. Dorsal; 214. Palpus. 215. *Zygiella x-notata* (Clerck 1757), palpus. 216. *Nicolepeira transversalis* (Nicolet 1849), palpus. Scale lines = 1 mm; palpi, 0.1 mm.

- into point at each end (Fig. 194); max. 4 mm; holarctic, or introduced to NE U. S.
 *Cercidia prominens*
- Abdomen and M otherwise 10
- 10(9) M with one narrow branch (Fig. 195); abdomen with discrete black patches and bands
 (as in female, Fig. 138); max. 7 mm; 5 sp., Guyanas to N Argentina *Dubiepeira*
- M otherwise 11
- 11(10) M with two flagellate projections on shared base (Figs. 196–200) 12
- M without paired, flagellate projections (Figs. 203–207) 16
- 12(11) A asymmetrical, circular (Fig. 196); abdomen short, oval, with median ventral white
 line (as in female, Figs. 120, 121); max. 8 mm; 41 sp., many social; U. S. to S Chile,
 W Indies *Metepeira*
- A rod-shaped (Figs. 197–200) 13
- 13(12) Abdomen with humps (as in female, Fig. 126, 146) 14
- Abdomen oval, without humps (as in female, Figs. 128, 142) 15
- 14(13) Abdomen diamond-shaped (as in female, Fig. 126); legs thin; A dividing palpus (Fig.
 197); max. 4 mm; 1 sp., Amazon to Bolivia, Bahia, Brazil *Madrepeira amazonica*
- Abdomen with prominent humps, slightly longer than wide (as in female Fig. 146); A
 terminal (Fig. 200); max. 4 mm; 4 sp., Honduras to S Brazil *Tatepeira*
- 15(13) Abdomen narrowly oval, length about 1.6 times its width (as in female Fig. 142); palpus
 (Fig. 198); max 3.5 mm; eye region black; 5 sp., Amazon area .. (in part) *Amazonpeira*
- Abdomen wider, length about 1.3 times its width; (as in female Fig. 128, 131); palpus
 (Fig. 199); 3.5 to 6 mm; N Am. abdomen with ventral, median white line; max. 9 mm;
 13 sp., Alaska to Argentina *Aculepeira*
- 16(11) ME region usually black on glossy carapace; glossy abdomen with two longitudinal
 black bands or four dark patches; carapace glossy (as in female Figs. 100, 103); ho-
 larctic 17
- ME region light (as in female Figs. 151, 152) on setose carapace; abdomen setose (as
 in female Fig. 151, 152) 18
- 17(16) First coxa with hook (Fig. 201); macrosetae of unequal thickness; palpus (Fig. 202);
 max. 6 mm; 2 sp., E Canada, U. S. *Singa*
- First coxa without hook; palpus (Fig. 203); max. 4 mm; 5 sp., Alaska to S U. S.
 *Hypsosinga*
- 18(16) Metatarsi and tarsi longer than patellae and tibiae; abdomen elongated, often with an-
 terior median tubercle and median ventral white streak (as in female, Fig. 149, 151);
 M with two projections, each turned toward Y (Fig. 204); max. 7 mm; 11 sp., S Canada
 to Argentina, W. Indies. *Larinia*
- Metatarsi and tarsi shorter than patellae and tibiae; abdomen rounded anteriorly, oval
 to round, often with humps; M with teeth or points (Figs. 205–207); max. 10 mm; ca.
 165 sp., Alaska to Chile, W Indies (most) *Araneus*
- 19(1) Third tibia with anterior feathery trichobothria thoracic region usually high, with slop-
 ing cephalic region (as in female Fig. 2); palpus (Fig. 317); max. ca. 8 mm; ca. 20 sp.,
 E Canada to Argentina, W Indies *Mangora*
- Third tibia without feathery trichobothria (Figs. 185, 208) 20
- 20(19) Median apophysis soft, white, worm-shaped (Figs. 209–212) 21
- M sclerotized with edge or spines (Figs. 206, 207, 215) 22
- 21(20) M in longitudinal position on side of palpus (Figs. 209, 210); PME separated by more
 than their diameter (Fig. 208); max. ca. 9 mm; ca. 100 sp., Canada to Argentina, W
 Indies *Eustala*
- M in transverse position (Figs. 211, 212); PME separated by less than their diameter
 (as in female, Fig. 18); max. 8 mm; 88 sp., S U. S. to Argentina, W Indies
 (in part) *Metazygia*
- 22(20) Palpal tibia cone-shaped, as long or longer than wide (Figs. 214–216) 23
- Palpal tibia bowl-shaped, as wide as long or shorter, distal margin indented, asymmet-
 rical (Figs. 205, 211, 221) 25

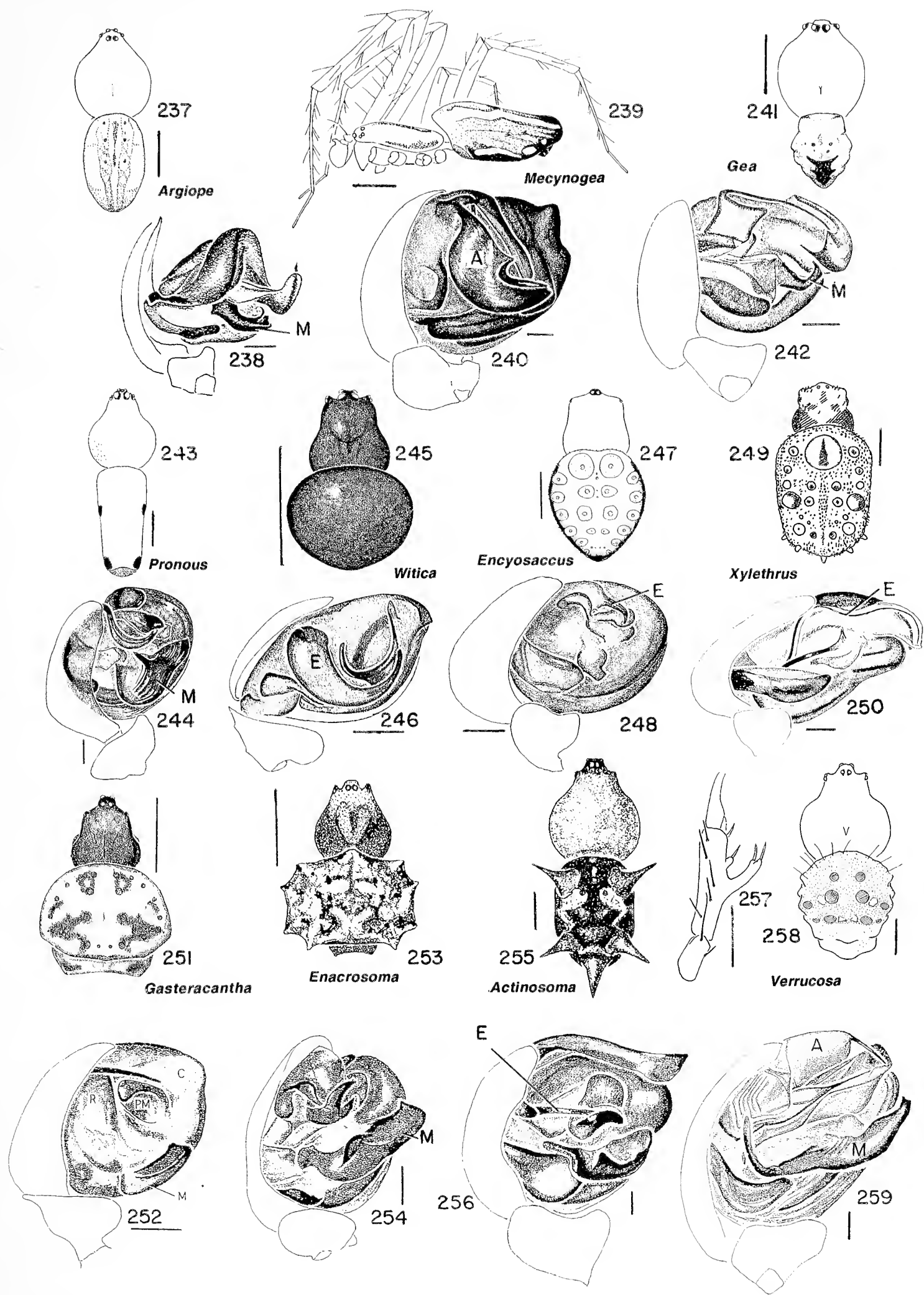


Figures 217–236.—Males: 217–219. *Hypognatha cryptocephala* Mello-Leitão 1947. 217. Eyes, dorsal; 218. Eyes, clypeus, chelicerae and right palpus; 219. Palpus.. 220, 221. *Acanthepeira stellata* (Walckenaer 1805). 220. Dorsal; 221. Palpus. 222, 223. *Chaetacis picta* (C.L. Koch 1836). 222. Dorsal; 223. Palpus. 224. *Micrathena* sp., lateral. 225, 227, 228. *M. pupa* Simon 1897. 225. Dorsal; 227, 228. Palpus; 227. Mesal; 228. Lateral. 226. *M. vigorsi* (Perty 1833), dorsal. 229, 230. *Edricus productus* O. P.-Cambridge 1896. 229. Dorsal; 230. Palpus.. 231, 232. *Parawixia matiapa* Levi 1992. 231. Dorsal; 232. Palpus.. 233, 234. *Wixia abdominalis* (O. P.-Cambridge 1882). 233. Lateral; 234. Palpus.. 235, 236. *Scoloderus nigriceps* (O. P.-Cambridge 1895). 235. Dorsal; 236. Palpus. Scale lines = 1 mm; palpi, 0.1 mm.

23(22)	Carapace bulging (Fig. 213); abdomen with glossy scute (Fig. 213); palpus (Fig. 214); max. 3 mm; Venezuela to Bolivia	<i>Aspidolasius branicki</i>
—	Carapace normal shape; abdomen soft	24
24(23)	Abdomen oval, longer than wide, without humps (as in female, Fig. 171); palpus (Fig. 215); max. 6 mm; 5 sp., Alaska to U. S., introduced in Argentina, Chile	(in part) <i>Zygiella</i>
—	Abdomen as wide as long with humps (as in female, Fig. 104); palpus (Fig. 216); max. 3 mm; Chile	<i>Nicolepeira transversalis</i>
25(22)	Carapace with projections (Fig. 217), pairs of dimples (Fig. 224), tubercles (as in female, Figs. 25, 27), bulges (Fig. 231), spines or denticles (Fig. 222), or elongated (Fig. 229)	26
—	Carapace not so modified (Figs. 237, 243, 247, 255)	34
26(25)	Clypeus with anterior projections (Figs. 217, 218); sternum with posterior notch holding extension from genital area (as in female, Fig. 29); abdomen with turtle-like scutes (as in female, Fig. 30); palpus (Fig. 219); max. 5 mm; 35 sp., Mexico to N Argentina	<i>Hypognatha</i>
—	Carapace, sternum and abdomen otherwise	27
27(26)	Carapace with denticles around sides and spines or denticles on each side in LE region (Fig. 222); palpus (Fig. 223); max. 4 mm; 9 sp., S Mexico to Paraguay	<i>Chaetacis</i>
—	Carapace otherwise	28
28(27)	Carapace with pairs of dimples (Fig. 224), often with a thoracic bulge; abdomen dorsally flattened, rectangular, barrel or violin-shaped, with thin scutum (Figs. 224–226); modified P (Fig. 228); lung covers usually have a stridulating area (as in female, Fig. 47); max. 8 mm; 104 sp., S Canada to Argentina, W Indies	(in part) <i>Micrathena</i>
—	Carapace without pairs of dimples; abdomen otherwise; without stridulating area on lung covers	29
29(28)	LE on side of projection (Fig. 220); abdomen surrounded by large spines, including anterior, median spine (Fig. 220); palpal sclerites partly covered by large Y (Fig. 221); max. 11 mm; 4 sp., Canada to C America, W Indies	<i>Acanthepeira</i>
—	LE not on sides of projection; abdomen usually without anterior, median spine; palpus otherwise	30
30(29)	Carapace elongated posteriorly (Fig. 229); palpus with large M (Fig. 230); max. 10 mm; 2 sp., Mexico to Ecuador	<i>Edricus</i>
—	Carapace with normal outline (Figs. 231, 233, 235)	31
31(30)	Carapace posteriorly with two branched tubercles (Fig. 315); palpus (Fig. 314); max. 2 mm; 45 sp., NE U. S. to Argentina	<i>Mastophora</i>
—	Carapace with bulges or swellings (Figs. 231, 233, 235)	32
32(31)	Carapace with two bulges (Fig. 231); PME facing dorsally (Fig. 231); abdomen attached on its anterior end (Fig. 231); M longer than wide, projecting (Fig. 232); max. 19 mm; 27 sp., Baja California to Argentina, W Indies	(in part) <i>Parawixia</i>
—	Carapace with one bulge; PME facing dorsolaterally (Fig. 235); abdomen attached near its middle or posterior end (Figs. 233, 235);	33
33(32)	Abdomen length more than 3 times its width, attached on its posterior third, held vertically (Fig. 233); clypeus high (Fig. 233); M complex (Fig. 234); max. 6 mm; Guyanas to Bolivia	<i>Wixia abdominalis</i>
—	Abdomen as wide as long, attached near middle (Fig. 235); M wide, flat (Fig. 236); max. 3 mm; 5 sp., Florida to N Argentina, W Indies	<i>Scoloderus</i>

→

Figures 237–259.—Males: 237. *Argiope argentata* (Fabricius 1775), dorsal. 238. *A. savignyi* Levi, 1968. Palpus. 239, 240. *Mecynogea lemniscata* (Walckenaer 1841). 239. Lateral; 240. Palpus. 241, 242. *Gea heptagon* (Hentz 1850). 241. Dorsal; 242. Palpus.. 243. *Pronous intus* Levi 1995, dorsal. 244. *P. felipe*



Levi 1995, palpus. 245, 246. *Witica crassicauda* (Keyserling 1865). 245. Dorsal; 246. Palpus.. 247. 248. *Encyosaccus sexmaculatus* Simon 1895. 247. Dorsal; 248. Palpus. 249. 250. *Xylethrus scrupus* Simon 1895. 249. Dorsal; 250. Palpus. 251, 252. *Gasteracantha cancriformis* (Linné 1767). 251. Dorsal; 252. Palpus. 253, 254. *Enacrosoma frenca* Levi 1996. 253. Dorsal; 254. Palpus. 255, 256. *Actinosoma pentacanthum* (Walckenaer 1841). 255. Dorsal; 256. Palpus. 257–259. *Verrucosa arenata* (Walckenaer 1841). 257. Left tibia; 258. Dorsal; 259. Palpus. Scale lines = 1 mm; palpi = 0.1 mm.

34(25) Posterior row of eyes procurved (Figs. 237, 241); lateral eyes anterior of medians in dorsal view 35

— Posterior eye row straight or recurved, as viewed from above (Figs. 243, 245, 247, 258) 38

35(34) Carapace with median dark line and thoracic region with dark sides (Fig. 239) 36

— Carapace without line (Figs. 237, 241) 37

36(35) Abdomen pattern with median, dorsal black mark (Fig. 239); A biforked (Fig. 240); max. 8 mm; 9 sp., SE U. S. to Chile, W Indies *Mecynogea*

— Abdomen without median black marks (Fig. 297); A not biforked (Fig. 298); max. 5 mm; 3 sp., Mexico to N Argentina (in part) *Manogea*

37(35) Distance between PME less than distance to PLE (Fig. 237); M with spur (Fig. 238); max. 8 mm; 6 sp., Canada to Chile, W Indies *Argiope*

— Distance between PE equal (Fig. 241); M without spur (Fig. 242); max. 4 mm; U. S. to Argentina, introduced from SW Pacific? *Gea heptagon*

38(34) Abdomen modified with dorsal sclerotized areas (Figs. 243, 245), more than two tubercles (Fig. 251, 253) or posteriorly elongated (Figs. 263, 264) 39

— Abdomen, oval, spherical, tubular, with at most 2 humps and an anterior median or posterior median bulge or a posterior notch (Figs. 275, 277, 284, 287) 56

39(38) PME twice diameter AME and facing dorsolaterally (Fig. 243) and abdomen orange, soft, rectangular with pairs of black tubercles (Fig. 243); M with median spine pointing at Y (Fig. 244); max. 5 mm; 14 sp., Mexico to Argentina *Pronous*

— PME diameter subequal with other eyes; abdomen and palpus otherwise 40

40(39) Abdomen shield-shaped with sclerotized, tortoise pattern, or slightly sclerotized (Fig. 311, or as in female, Fig. 28); palp without radix (Fig. 312); max. 3.5mm; ca. 9 sp., Panama to N Argentina (in part) *Testudinaria*

— Abdomen otherwise 41

41(40) Abdomen subspherical covered by glossy scutum (Figs. 213, 245) 42

— Abdomen otherwise 43

42(41) Abdomen completely covered by glossy scutum (Figs. 245); comma-shaped E (Fig. 246); max. 2 mm; 2 sp., Mexico to Guyanas, Peru, W. Indies *Witica*

— Abdomen only partly covered by scutum (Fig. 213); E coiled (Fig. 214); max. 3 mm; Venezuela to Bolivia *Aspidolasius branicki*

43(41) Abdomen dorsally with pairs of sclerotized round disks, some large (other than paired muscle sclerites), but without tubercles on side of abdomen (Figs. 247, 249) 44

— Abdomen without sclerotized disks, or with disks and tubercles on sides (Figs. 251, 253, 255, 258) 45

44(43) Abdomen shield-shaped (Fig. 247); E short (Fig. 248); max. 4 mm; upper Amazon ..
..... *Encyosaccus sexmaculatus*

— Abdomen square to rectangular with denticles around edge (Fig. 249); E long, filiform (Fig. 250); max. 5 mm; 5 sp., Mexico to S Brazil, Jamaica *Xylethrus*

45(43) Abdomen with five spines (Fig. 255); E straight rod (Fig. 256); max. 7 mm; Amazon area to Argentina *Actinosoma pentacanthum*

— Abdomen otherwise 46

46(45) ME region projecting (Fig. 251); abdomen a half-circle in front, truncate behind (Fig. 251); PM circular and in center (Fig. 25); max. 3 mm; SE U. S. to Argentina, W Indies
..... *Gasteracantha cancriformis*

— ME region normal, slightly prolonged; abdomen otherwise (Figs. 253, 258); palp otherwise 47

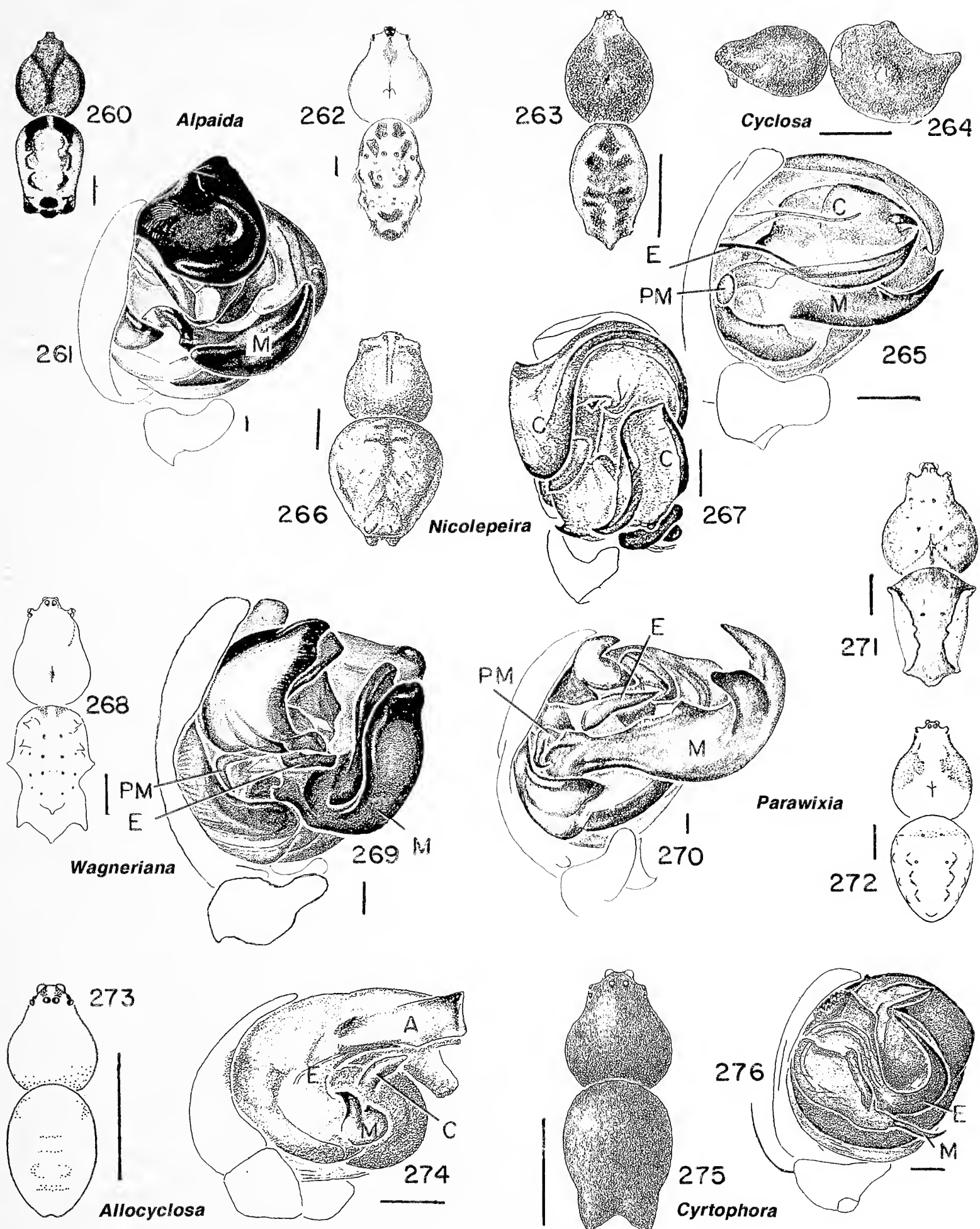
47(46) Abdomen short, anteriorly semispherical with posterior tubercles on humps (as in female Fig. 69); palpus (Fig. 316); max. 3 mm; SE U. S. *Colphepeira catawba*

— Abdomen otherwise 48

48(47) Carapace glossy, dorsal area of abdomen or whole abdomen glossy 49

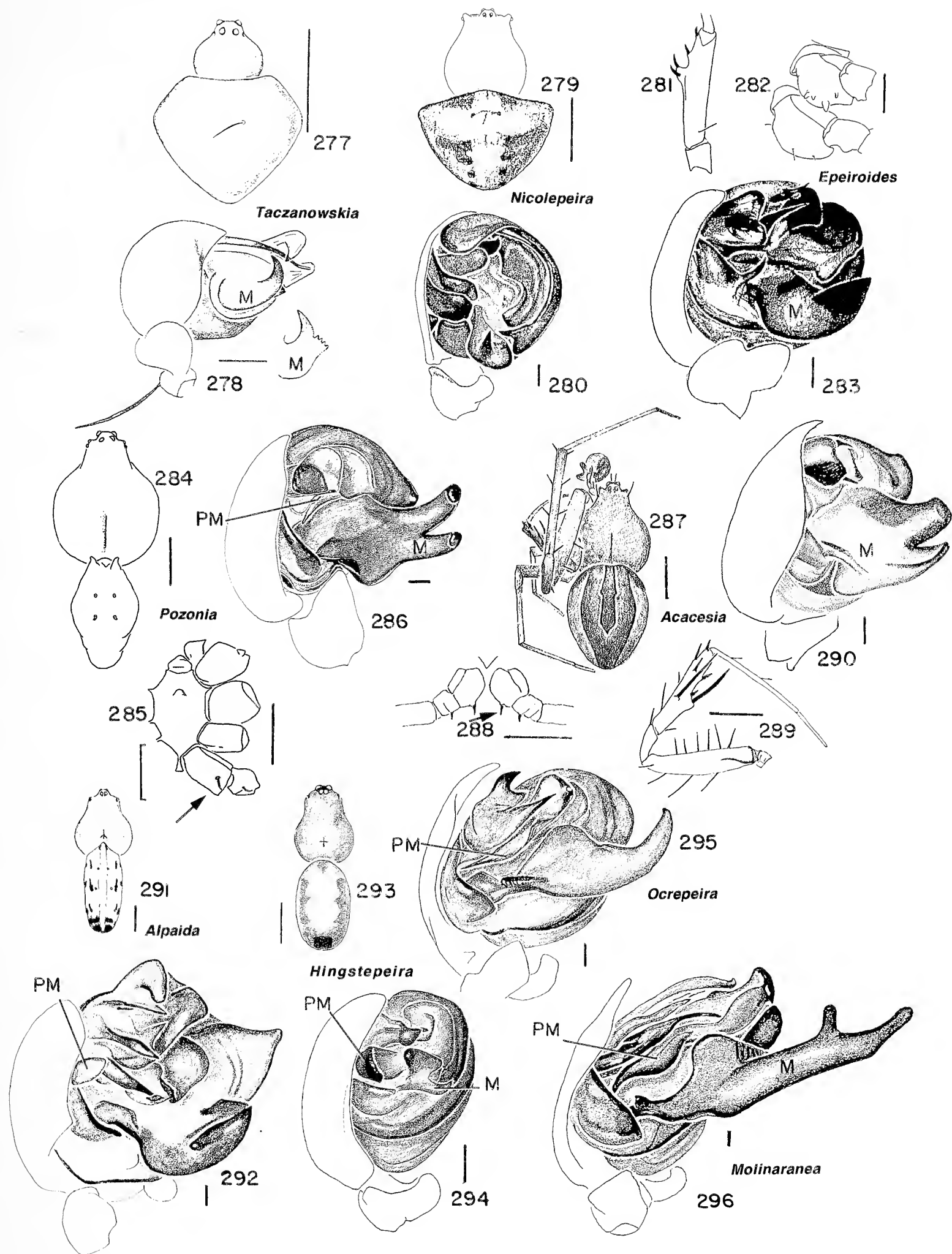
— Carapace, abdomen soft or setose 51

49(48) Abdomen dorsally flattened (Fig. 224), thin scutum; pleats on sides (Fig. 224), rect-



Figures 260–279.—Males: 260, 261. *Alpaida truncata* (Keyserling 1865). 260. Dorsal; 261. Palpus. 262. *A. alticeps* (Keyserling 1880), dorsal. 263. *Cyclosa berlandi* Levi 1999, dorsal. 264, 265. *C. turbinata* (Walckenaer 1841). 264. Dorsolateral; 265. Palpus. 266, 267. *Nicolepeira bicaudata* (Nicolet 1849). 266. Dorsal; 267. Palpus. Figs. 268, 269. *Wagneriana tauricornis* (O. P.-Cambridge 1889). 268. Dorsal; 269. Palpus. 270. *Parawixia nesophila* Chamberlin & Ivie 1936, palpus. 271. *P. hypocrita* (O. P.-Cambridge 1889), dorsal. 272. *P. porvenir* Levi 1992, dorsal. 273, 274. *Allocyclosa bifurca* (McCook 1887). 273. Dorsal; 274. Palpus. 275, 276. *Cyrtophora citricola* (Forskål 1775). 275. Dorsal; 276. Palpus. Scale lines = 1 mm; palpi = 0.1 mm.

	angular, trapezoid, barrel, violin-shaped, rarely with spines (Figs. 224–226); booklung covers usually a stridulating area (as in female, Fig. 47); palpus (Figs. 227–228); max. 8 mm; 104 sp., S Canada to Argentina, W Indies (in part) <i>Micrathena</i>	
—	Abdomen otherwise (Figs. 258, 260, 262); lung covers never with stridulating area	50
50(49)	Abdomen trapezoidal narrower behind, sides and posterior with dark-capped, white tubercles (Fig. 258); second tibia with spur (Fig. 257); M with long, proximal projection pointing toward A (Fig. 259); max. ca. 10 mm; ca. 15 sp., E U. S. to Argentina, W Indies <i>Verrucosa</i>	
—	Abdomen oval, glossy with some lateral or posterior tubercles or anterior teeth (Figs. 260, 262); M without proximal projection (Fig. 261); max. 11 mm; 134 sp., S Mexico to Argentina, W Indies (a few) <i>Alpaida</i>	
51(48)	Abdomen wider than long, rectangular (Fig. 253); M rectangular, distally truncate (Fig. 254); max. 3 mm; 6 sp., Mexico to São Paulo State, Brazil <i>Enacrosoma</i>	
—	Abdomen as long as wide or longer than wide	52
52(51)	Abdomen elongate, pointed, overhanging spinnerets (Figs. 264); tubercles, if present, dorsal or posterior (Fig. 264) and large oval C, with gutter holding filiform E above M; PM straight with pocket at end, (Fig. 265); max. 5 mm; 51 sp., Alaska to S Argentina, W Indies (in part) <i>Cyclosa</i>	
—	Abdomen not pointed and overhanging spinnerets, or with paired lateral tubercles (Figs. 266, 268, 271, 272); and palpus otherwise (Figs. 267, 269, 270)	53
53(52)	PM present (Figs. 269, 270)	55
—	Without PM (Figs. 267, 313)	54
54(53)	Carapace and abdomen with little dark pigment; without four posterior-facing tubercles, M with row of denticles and two flagellum-shaped projections from joint base (Fig. 313); C small; total length; max. 3 mm; 14 sp., E U. S. to N Argentina, W Indies (in part) <i>Kaira</i>	
—	Abdomen pigmented, with two to four posterior facing tubercles (Fig. 266); M otherwise; C very large (Fig. 267); max. 5 mm; Chile <i>Nicolepeira bicaudata</i>	
55(53)	Abdomen rectangular with paired tubercles and posterior median tubercle (Fig. 268); E knife-shaped, M projecting low, toward 4h in left palpus (Fig. 269); cephalic area pale, thoracic area dark, glossy; max. 11 mm; 39 sp., SE U. S. to Argentina, W Indies <i>Wagneriana</i>	
—	Abdomen round to trapezoidal with paired tubercles (Figs. 271, 272); E bullet-shaped (Fig. 270); M projecting distally at 3 o'clock of left palpus (Fig. 270); sides of carapace setose; max. 19 mm; 27 sp., Baja California to Argentina, W Indies (in part) <i>Parawixia</i>	
56(38)	Abdomen oval with posterior notch (Figs. 273, 275); social sp., male uncommon . .	57
—	Abdomen without posterior notch (Figs. 277, 284, 29	58
57(56)	Light-colored (Fig. 273); palpus (Fig. 274); max. 2 mm; Florida, Baja California to Panama, W Indies <i>Allocyclosa bifurca</i>	
—	Dark-colored (Fig. 275); palpus (Fig. 276); max. 3 mm; tropical, introduced <i>Cyrtophora citricola</i>	
58(56)	Abdomen wider than long (Figs. 277, 279)	59
—	Abdomen longer than wide (Figs. 284, 293)	61
59(58)	Third coxa with tubercles (Fig. 282); second tibia branching (Fig. 281), palpus with median apophysis having a keel (Fig. 283); max. 5 mm; Costa Rica to Bahia, Brazil <i>Epeiroides bahiensis</i>	
—	Third coxa without tubercles	60
60(59)	Tropical; one tarsal claw longer than other (as in female, Fig. 20); M with one spine (Fig. 278); max. 2 mm; 4 sp., Colombia to S Brazil <i>Taczanowskia</i>	
—	Temperate South America; tarsal claws equal in length; palpus (Fig. 280); max. 5 mm; Chile. <i>Nicolepeira flavifrons</i>	
61(58)	Paramedian apophysis present (Fig. 286, 292, 296), or fourth coxa with short macroseta (Figs. 285, 288)	62



Figures 277–296.—Males: 277, 278. *Taczanowskia striata* Keyserling 1880. 277. Dorsal; 278. Palpus. 279, 280. *Nicolepeira flavifrons* (Nicolet 1849). 279. Dorsal; 280. Palpus. 281–283. *Epeiroides bahiensis* Keyserling 1885; 281, left second tibia. 282. Third and fourth left coxae; 283. Palpus. 284–286. *Pozonia nigroventris* (Bryant 1936). 284. Dorsal; 285. Sternum and left coxae; 286. Palpus. 287–290. *Acacesia hamata* (Hentz 1847). 287. Dorsal; 288. Fourth coxae and trochanters; 289. Left second leg; 290. Palpus. 291, 292. *Alpaida grayi* (Blackwall 1863). 291. Dorsal; 292. Palpus. 293, 294. *Hingstepeira folisecens* (Hingston 1932). 293. Dorsal; 294. Palpus. 295. *Ocrepeira covillei* Levi, 1993, palpus. 296. *Molinaranea magellanica* (Walckenaer 1847), palpus. Scale lines = 1 mm; palpi = 0.1 mm.

— Without PM or PM not visible; fourth coxae never with macroseta. 69

62(61) Sternum with median tubercle (Fig. 285); M biforked (Fig. 286); abdomen with anterior tubercles (Fig. 284); max. 7 mm; 3 sp., S Mexico to S Brazil, W Indies *Pozonia*

— Sternum otherwise 63

63(62) PME face dorsolaterally (Figs. 287, as in female Fig. 119) 64

— PME face dorsally (Figs. 291, 293) 65

64(63) Abdomen dorsally with two pairs of black, longitudinal, lines approaching each other at ends, without or with lateral humps (Fig. 287); second tibia branched (Fig. 289); M biforked (Fig. 290); max. 7 mm; 8 sp., E U. S. to N Argentina, W Indies *Acacesia*

— Abdomen without lines, pair of humps as in female (as in female, Fig. 119); PM usually pointed (Fig. 295); max. 9 mm; 67 sp., E U. S. to Chile, W Indies . . (in part) *Ocrepeira*

65(63) Abdomen oval, with distinct black patch posteriorly (Fig. 293) and on venter; small M (Fig. 294); max. 5 mm; 4 sp., Guyanas to C Amazon area *Hingstepeira*

— Abdomen and palpus otherwise 66

66(65) Abdomen usually overhanging spinnerets (Figs. 263, 264, as in female, Figs. 79, 80); narrow head, PME adjacent (Fig. 263); large C carrying filiform E in a gutter close to M (Fig. 265); max. 5 mm; 51 sp., Alaska to S Argentina, W Indies . . . (in part) *Cyclosa*

— Abdomen and palpus otherwise 67

67(66) Carapace, abdomen glossy (Fig. 260, 291); ME area often black on yellow carapace; PM with enlargement at end (Figs. 292); max. 11 mm; 134 sp., S Mexico to Argentina, W Indies (in part) *Alpaida*

— Carapace, abdomen setose 68

68(67) Temperate South America; PM conical, pointed (Fig. 296); M biforked (Fig. 296); max. 10 mm; 7 sp. *Molinaranea*

— Cerrado savanna, S Brazil, Paraguay; PM round, M distally truncate (Fig. 191); max. 19 mm *Parawixia bistriata*

69(61) Palpus with sclerites small, E supported by A, M a small pointed projection (Figs. 298, 300); PME straight (Figs. 297, 299) 70

— Palpus with sclerites large; M otherwise (Figs. 302, 304, 307, 308); PME recurved 71

70(69) Abdomen oval, widest anteriorly, often with thin, white, longitudinal lines (Fig. 299); palpus (Fig. 300); max. 4 mm; 4 sp., Mexico to Argentina, W Indies *Kapogea*

— Abdomen oval, widest in middle, with longitudinal, light bands (Fig. 297); palpus (Fig. 298); max. 5 mm; 3 sp., Mexico to N Argentina (in part) *Manogea*

71(69) Abdomen reddish with white patches (Fig. 301); M projecting, T-shaped, (Fig. 302); max. 4 mm; 3 sp., Honduras to Rio de Janeiro State, Brazil *Spilasma*

— Abdomen and M otherwise 72

72(71) Mesal side of palpus covered by a shield (Figs. 305, 306); max. 5 mm; 4 sp., Mexico, C Amer., W Indies. *Lewisipeira*

— Palpus without shield 73

73(72) M with two flagellum-shaped projections from a joint base (Figs. 310, 313); less than 3 mm 74

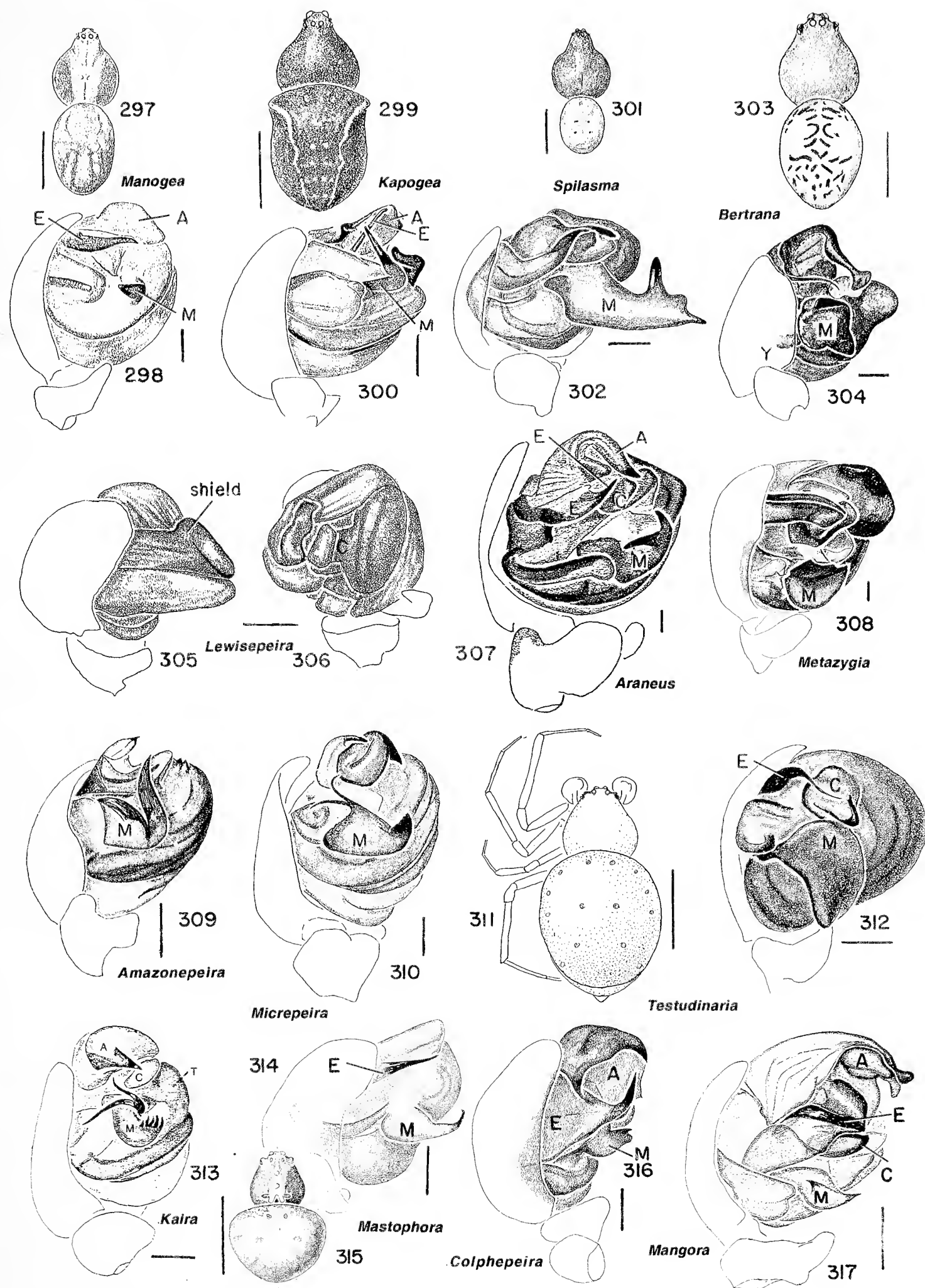
— M without or only one such spines (Figs. 307, 308, 312); most more than 4 mm total length 75

74(73) Abdomen spherical (as in female, Fig. 164); M with spine or with only indistinct teeth (Fig. 310); max. 3 mm; 7 sp., Costa Rica to Mato Grosso *Micrepeira*

— Abdomen oval to shield-shaped; M with a row of long, sharp teeth (Fig. 313); total length; max. 3 mm; 14 sp., E U. S. to N Argentina, W Indies *Kaira*

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Figures 297–313.—Males: 297, 298. *Manogea porracea* (C.L. Koch 1839). 297. Dorsal; 298. Palpus. 299, 300. *Kapogea alayoi* (Archer 1958). 299. Dorsal; 300. Palpus. 301, 302. *Spilasma duodecimguttata* (Keyserling 1880). 301. Dorsal; 302. Palpus. 303, 304. *Bertrana striolata* Keyserling 1884. 303, dorsal.



304. Palpus. 305, 306. *Lewisipeira farri* (Archer 1958), palpus. 305. Mesal; 306. Ventral. 307. *Araneus gemma* (McCook 1888), palpus. 308. *Metazygia laticeps* (O.P.-Cambridge 1889), palpus. 309. *Amazonipeira herrera* Levi 1989, palpus. 310. *Micrepeira hoeferi* Levi 1995, palpus. 311, 312. *Testudinaria* sp. 311. Dorsal; 312. Palpus. 313. *Kaira alba* (Hentz 1850), palpus. 314, 315. *Mastophora gasteracanthoides* (Nicolet 1849). 314. Palpus; 315. Male. 316. *Colphepeira catawba* Banks 1911, palpus. 317. *Mangora fascialata* Franganillo 1936, palpus. Scale lines = 1 mm; palpi = 0.1 mm.

75(73)	M distally with one wide S-shaped, curved projection; eye region black (Fig. 309), abdomen narrowly oval (as in female, Fig.142); max. 4 mm; Amazon area	<i>Amazonopeira herrera</i>
—	M otherwise	76
76(75)	PME less than their diameter apart; carapace and abdomen glossy, abdomen oval without humps, widest in middle, slightly flattened (as in female, Figs. 158, 162); M without teeth, rarely with spines (Figs. 308); max. 8 mm; 88 sp., S U. S. to Argentina, W Indies	(in part) <i>Metazygia</i>
—	PME their diameter or more apart;	77
77(76)	Abdomen shield-shaped, flattened to oval; legs thin (Fig. 311); M without teeth or spines, radix lacking (Fig. 312); max. 3.5 mm; 9 sp., Panama to N Argentina	(in part) <i>Testudinaria</i>
—	Abdomen otherwise; M with or without spines	78
78(77)	Abdomen usually with humps; M with two recurved spines (Fig. 307); max. 10 mm; North American	(a few) <i>Araneus</i>
—	Abdomen without humps; M otherwise	79
79(78)	Costa Rica to S Brazil; abdomen spherical (Fig. 303); max 3 mm; 13 sp,	<i>Bertrana</i>
—	Alaska to US; abdomen oval; max. 7 mm; 5 sp.	(in part) <i>Zygiella</i>

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- Cardimia* Mello-Leitão 1939: 61, with the type species by monotypy, *C. eximia* Mello-Leitão 1939, (fig. 7) in the Museu Nacional, Rio de Janeiro, not examined. *Cardimia eximia* belongs to *Azilia* Keyserling 1882 and in the family Tetragnathidae. NEW SYNONYMY and NEW PLACEMENT.
- Epeirella* Mello-Leitão 1941: 149, with the type species by monotypy, *Epeirella tucumana* Mello-Leitão 1941 (pl. 7, fig. 31) in the Museu de la Plata, examined. *Epeirella tucumana* is an immature *Eriophora* Simon 1864 probably *E. edax* (Blackwall 1863). The immature specimen has dorsal abdominal pattern of broken black lines (as recently illustrated for immature *E. fuliginea* (C. L. Koch 1843) by Graf & Nentwig, 2001, fig. 1) and ventrally a horizontal black rectangle. *Epeirella* is a synonym of *Eriophora*. NEW SYNONYMY.
- Heterognatha* Nicolet 1849: 471, with the type species *H. chilensis* Nicolet 1849. *Heterognatha chilensis* has a lanceolate abdomen, lacks a male radix in the palpus, lacks araneid eye structure as in *Testudinaria*. Its placement is not known (Levi, in press).
- Melychiopharis*, Simon 1895: 907, figs. 972, 973, female, with the type species by monotypy, *M. cynips* Simon 1895. Males are located in the São Paulo and Porto Alegre, Brazil museums. The males place this species in the Theridiidae. NEW PLACEMENT.
- Nanduti* Mello-Leitão 1945: 241, with the type species by monotypy, *N. roseus* Mello-Leitão 1895 is a synonym of *Testudinaria*. NEW SYNONYMY.
- Spintharidius* Simon 1893: 327, contains three species. The type species, designated by Bonnet, 1958: 4121, is *M. rhomboidalis* Simon 1893. There are no illustrations and all specimens of this species are lost from the Museum National d'Histoire Naturelle, Paris. *Alpaida* O. P. –Cambridge 1889 might be a synonym of *Spintharidius*, but this is uncertain.
- Ursa* Simon 1895: 250, contains four species, one in America, all described from females. The type species designated by Bonnet, 1959: 4782 is *U. pulchra* Simon 1895 from Brazil, in the Museum National d'Histoire Naturelle, Paris, examined. It will be illustrated in Levi (in press).
- The as yet unrevised genus *Mangora* O. P.–Cambridge 1889 may have to be subdivided when all species are known.

APPENDIX 1.

The following genera are listed in catalogs as Araneidae (Platnick 1998) but are misplaced or synonyms.

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FOUR NEW SPECIES OF THE GENUS *LEPTONETA* (ARANEAE, LEPTONETIDAE) FROM TAIWAN

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ABSTRACT. The new species *Leptoneta changlini*, *L. huisunica*, *L. nigrabdomina* and *L. taiwanensis* are described and illustrated from Taiwan, and the natural history of *L. changlini* and *L. huisunica* is described. These species are only known from male specimens.

Keywords: Leptonetidae, *Leptoneta*, Taiwan, taxonomy, Asia

Leptonetids are very small (1–3 mm), haplogyne spiders with slender legs, which construct irregular sheet webs in leaf litter or within caves (Yaginuma 1986). Leptonetids usually have six eyes, with the four anterior eyes situated in a strongly recurved row with the two posterior eyes almost merged. In some species, the eyes may degenerate to four, two or even none (Song et al. 1999). Their genitalia are quite simple, and some individuals have two pairs of book lungs (Yaginuma 1986). The family has a worldwide distribution and contains more than 100 species belonging to 13 genera (Platnick 1998), of which 64 species of the genus *Leptoneta* (Brignoli 1972, 1979; Chen et al. 1984; Dresco 1987; Fage, 1913; Gertsch 1974; Komatsu 1957, 1970; Nishikawa 1982; Paik 1985; Paik et al. 1969; Platnick 1986; Song & Xu, 1986; Yaginuma 1962; Yin et al. 1984) are known from the United States, Mexico, the Mediterranean region and southeast Asia.

Leptonetids dwell mostly in caves or in leaf litter and thus are not easily found. No species of this family has previously been recorded from Taiwan. In a long term ecological research project conducted in Hui-Sun Experimental Forest Station (23.9° N, 120.6° E, elevation 1600–1800 m) in central Taiwan many pitfall traps were established to survey the invertebrate litter communities (Wang et al. 2001). In Taiwan pitfall traps have rarely been used in arachnofauna surveys. Consequently many undocumented ground spider species were found in these collections.

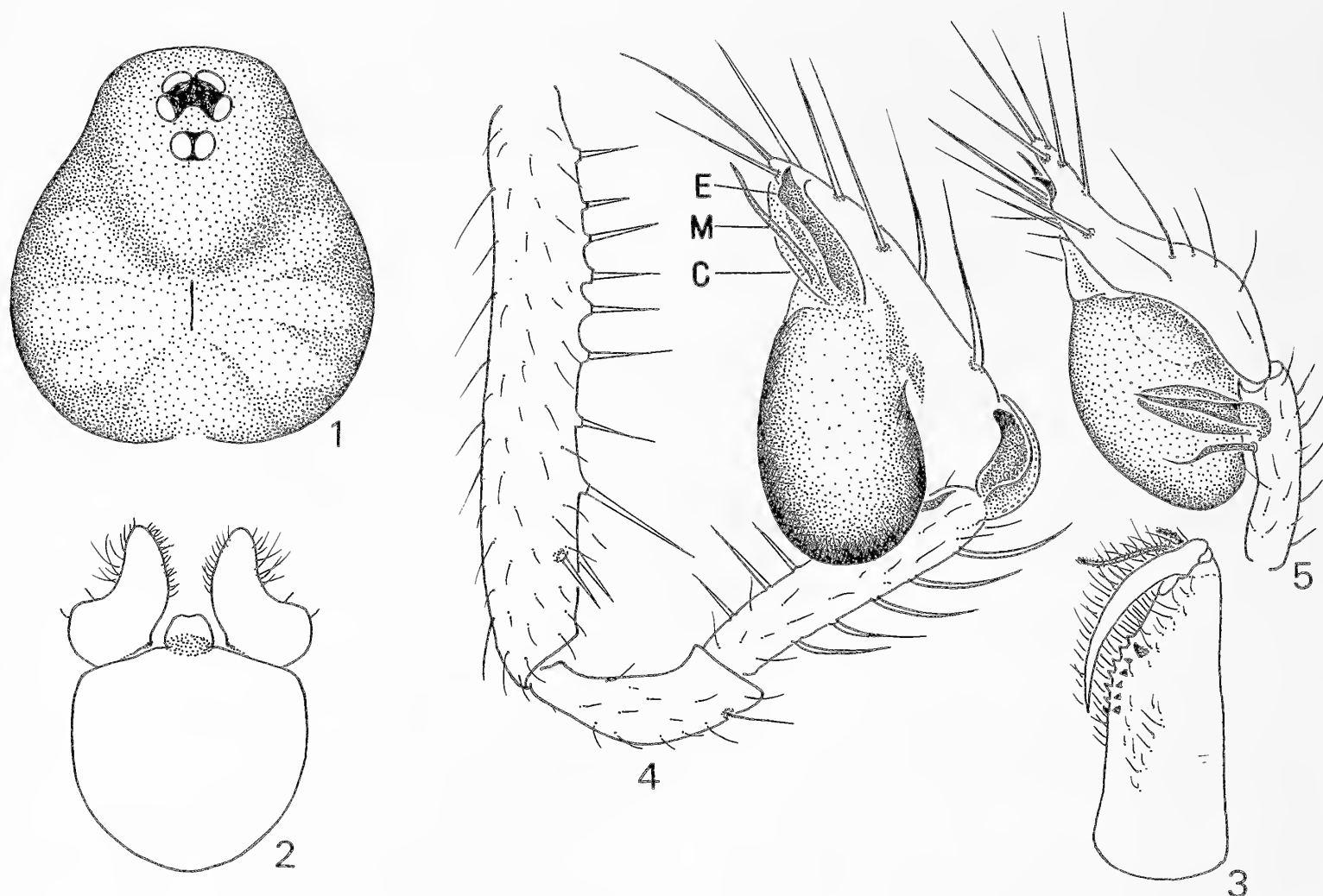
Among them are four species of *Leptoneta*, all of them are new to science.

In this paper we describe and illustrate these four species of *Leptoneta*. Pitfall traps were established in the study sites for a year and their contents collected every two months. This allowed us to draw natural history information from the temporal abundance pattern of the more abundant species, *L. changlini* and *L. huisunica*. In the species descriptions all measurements given are in millimeters. Size ranges of carapace and abdomen of the more abundant *L. changlini* and *L. husunica* were estimated from holotypes and paratypes. Palp and leg measurements are shown as: total length (femur, patella, tibia, metatarsus, tarsus). The type specimens used in this study are deposited in the National Museum of Natural Science, Taichung, Taiwan (NMNS-THU). Abbreviations used in this paper are: AER = anterior eye row; ALE = anterior lateral eye; AME = anterior median eye; EFL = length of eye field; PER = posterior eye row; PLE = posterior lateral eye; C = conductor of male palpal organ; E = embolus of male palpal organ; and M = median apophysis of male palpal organ.

TAXONOMY

Leptoneta changlini new species Figs. 1–5, 18–19

Material examined.—Holotype male, Hui-Sun Experimental Forest Station, Nantou County, Taiwan, April 1998, Hai-Yin Wu



Figures 1–5.—*Leptoneta changlini* new species: 1. Cephalothorax of male, dorsal view; 2. Endites, labium and sternum, ventral view; 3. Left chelicera, retrolateral view; 4. Left palp, retrolateral view; 5. Left palp, dorsal lateral view.

(NMNS-THU-Ar-990046); paratype male, same locality as holotype, December 1997, Hai-Yin Wu (NMNS-THU-Ar-990045); 1♂, same locality as holotype, April 1998, Sheng-Hai Wu (NMNS-THU-Ar-010101); 1♂, same locality as holotype, April 1998, Sheng-Hai Wu (NMNS-THU-Ar-010102).

Diagnosis.—The new species resembles *Leptoneta inabaensis* Nishikawa 1982, but differs by having the chelicera with seven promarginal teeth (Fig. 3), instead of eleven as in *L. inabaensis*; femur of palp with one row of long and thick ventral spines (Fig. 4), lacking in *L. inabaensis*; distal end of cymbium (tarsus) not branched, rather than branched as in *L. inabaensis*; and also by the different shape of laminae of palpal bulb (Figs. 4–5).

Description.—Male (holotype): Total length 1.41 ± 0.60 . Cephalothorax 0.61 ± 0.02 long, 0.53 ± 0.01 wide; abdomen 0.80 ± 0.09 long, 0.52 ± 0.03 wide. Carapace yellow, with gray brown margins, radial furrows and cervical grooves; fovea brown. Clypeus 0.13 high, slightly sloped anteriorly. Six eyes: ALE: PLE: PME (0.05: 0.05: 0.05); ALE–

PME 0.06, PLE–PME 0.01, PLE–PLE 0.05. Chelicera light yellow brown, with seven promarginal teeth and six retromarginal teeth. Endites and labium light yellow brown. Sternum and legs yellow. Measurements of palp and legs: palp 1.26 (0.49, 0.20, 0.22, –, 0.35); I (1.11, 1.82, 1.27, lost, lost); II (0.87, lost, lost, lost, lost); III 2.70 (0.73, 0.16, 0.68, 0.64, 0.49); IV (1.03, lost, lost, lost, lost). Abdomen oval, light yellow, with light brown hairs, dorsum with four light black brown transverse stripes posteriorly, forming four transverse folds. Palpal femur and tibia with many long spines dorsally and ventrally (Fig. 4), tibia with two projections, inner one leaf-like, outer one horn-shaped (Figs. 4, 5).

Female: Unknown.

Etymology.—The new species is named in honor of the Taiwanese arachnologist Dr. Changlin Li.

Natural history.—Specimens of *L. changlini* are quite abundant in the Hui-Sun Experimental Forest Area and mature male specimens were collected in pitfall traps during April and December (Table 1). Therefore, in

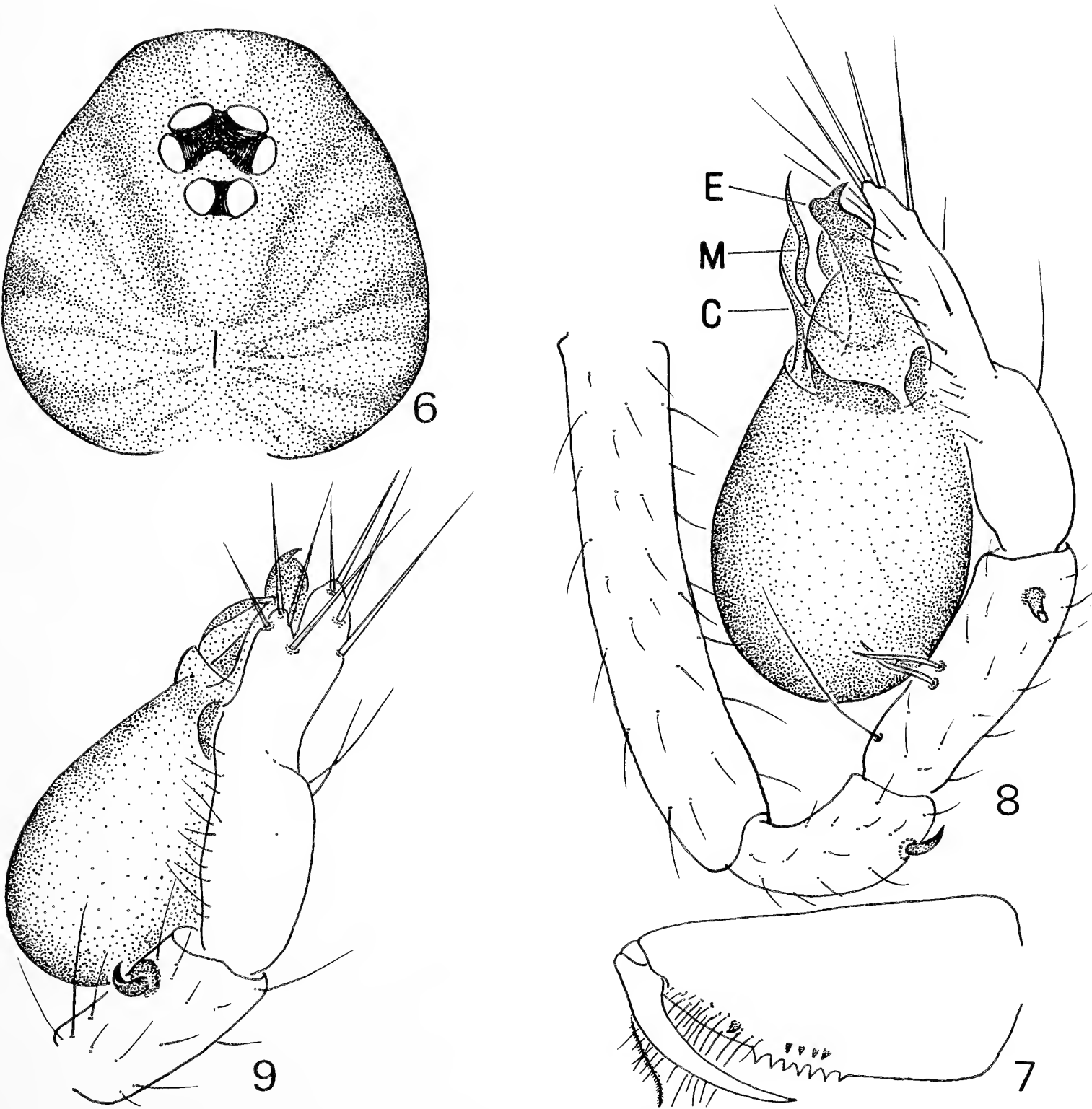
Table 1. Number of male *Leptoneta* specimens collected bimonthly between December 1997 and October 1998 from pitfall traps established in the Hui-Sun Experimental Forest Station.

	Dec. 1997	Feb. 1998	Apr. 1998	June 1998	Aug. 1998	Oct. 1998
<i>L. changlini</i>	1	0	4	0	0	0
<i>L. huisunica</i>	2	1	6	1	2	2

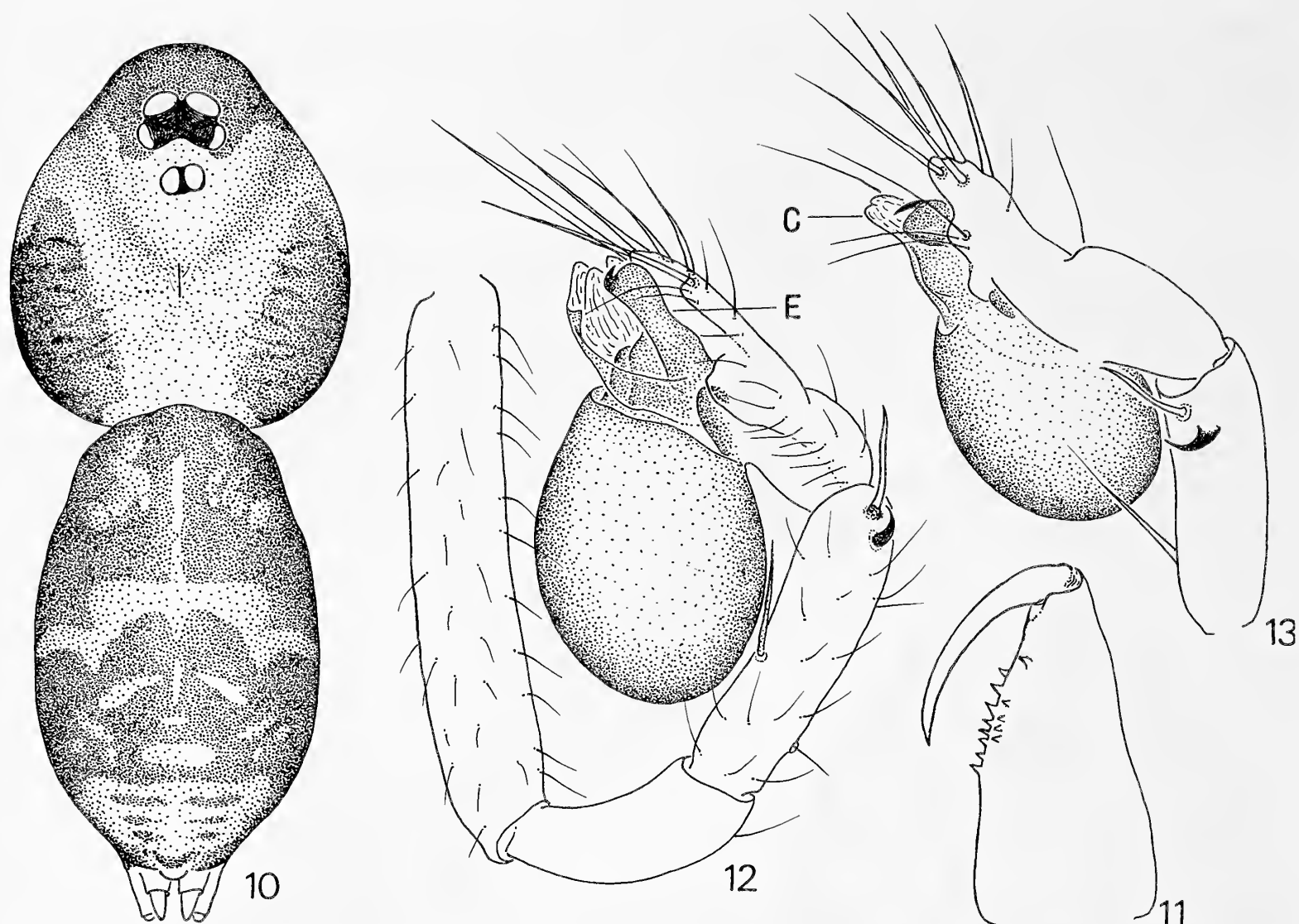
the central mountainous area of Taiwan *L. changlini* seems to reproduce during winter and spring.

Leptoneta huisunica new species
Figs. 6–9, 22

Material examined.—Holotype male, Hui-Sun Experimental Forest Station, Nantou County, Taiwan, April 1998 (NMNS-THU-Ar-990042), Sheng-Hai Wu; paratype male, same data as for holotype (NMNS-THU-Ar-990040); 1♂, same locality as holotype, December 1997 (NMNS-THU-Ar-990041), Hai-Yin Wu; 1♂, same locality as holotype, April



Figures 6–9.—*Leptoneta huisunica* new species: 6. Cephalothorax of male, dorsal view; 7. Left chelicera, retrolateral view; 8. Left palp, retrolateral view; 9. Left palp, dorsal lateral view.



Figures 10–13.—*Leptoneta nigrabdomina* new species: 10. Body of male, dorsal view; 11. Left chelicera, retrolateral view; 12. Left palp, outer lateral view; 13. Left palp, dorsal lateral view.

1998 (NMNS-THU-Ar-010103), Sheng-Hai Wu; 1♂, same locality as holotype, February 1998 (NMNS-THU-Ar-010104), Hai-Yin Wu; 1♂, same locality as holotype, February 1998 (NMNS-THU-Ar-010105), Hai-Yin Wu.

Diagnosis.—The new species is similar to *Leptoneta lingqiensis* Chen, Shen & Gao 1984 in the shape of the male palpal organ, but can be easily distinguished by the chelicera with 7 promarginal teeth and 5 retromarginal teeth (Fig. 7), instead of the 8 promarginal and 6 retromarginal teeth as in *L. lingqiensis*; male palpal tibia with one projection that is not distally branched, instead of 2 branches as in *L. lingqiensis*; and the different shape of laminae of the palpal bulb (Fig. 9).

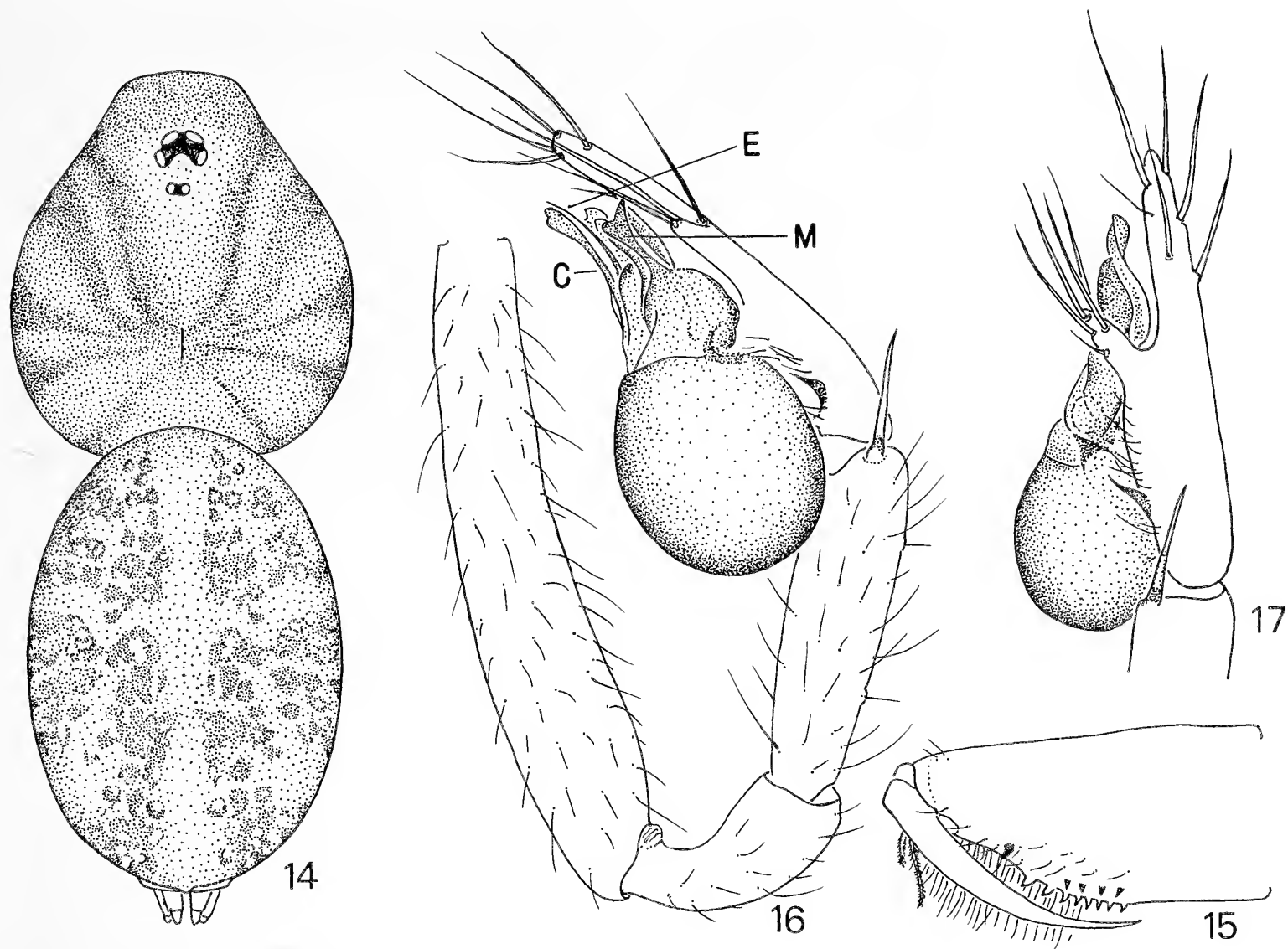
Description.—Male (holotype): Total length 1.58 ± 0.17 . Cephalothorax 0.67 ± 0.07 long, 0.60 ± 0.04 wide; abdomen 0.93 ± 0.09 long, 0.64 ± 0.06 wide. Carapace cream-colored, with light yellow brown margins, radial furrows and cervical grooves; fovea brown. Clypeus 0.14 high, not sloped and almost vertical. Six eyes: ALE: PLE: PME (0.08: 0.07:

0.05); ALE–PME 0.05, PLE–PME 0.01, PLE–PLE 0.09. Chelicera light yellow brown, with 7 teeth on promargin and 5 on retromargin. Endite, labium and sternum light yellow brown. Legs yellow, with several long and thin spines. Measurements of palp and legs: palp 1.01 (0.40, 0.13, 0.18, –, 0.30); I 4.44 (1.34, 0.20, 1.56, 0.81, 0.53); II (1.00, lost, lost, lost, lost); III (0.82, lost, lost, lost, lost); IV (1.11, lost, lost, lost, lost). Abdomen oval, dorsum gray yellow, with six light black brown transverse stripes postero-medially, venter yellow. Colulus thin and tipped. Palpal tibia with a single hook-like projection disto-laterally (Fig. 9); patella with a short dorsal spine (Fig. 8); cymbium with 2 distal branches (Fig. 9).

Female: Unknown.

Etymology.—The specific name refers to the type locality.

Natural history.—Among the four species of *Leptoneta* found within the Hui-Sun Experimental Forest Area, *L. huisunica* was the most abundant. Mature males were found in pitfall collections during almost all months



Figures 14–17.—*Leptoneta taiwanensis* new species: 14. Body of male, dorsal view; 15. Left chelicera, retrolateral view; 16. Left palp, retrolateral view; 17. Left palp, dorsal lateral view.

(Table 1). Therefore, *L. huisunica* seems to reproduce throughout the year in the central mountainous area of Taiwan.

Leptoneta nigrabdomina new species
Figs. 10–13, 23

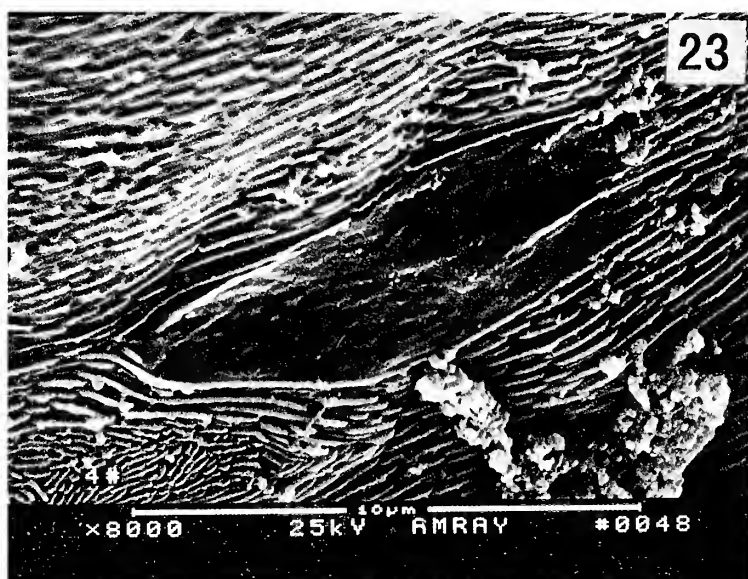
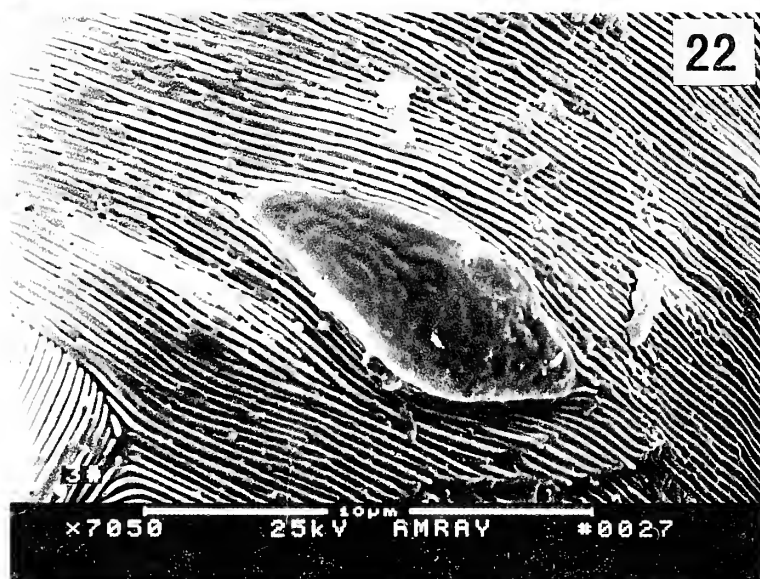
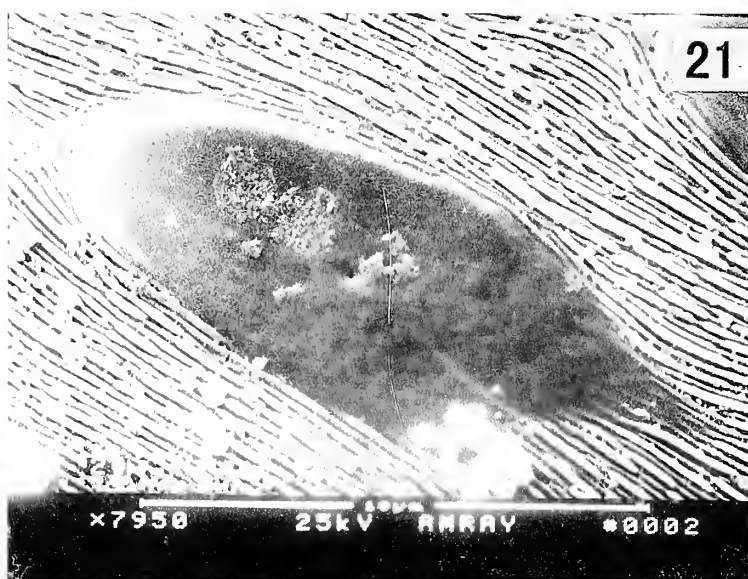
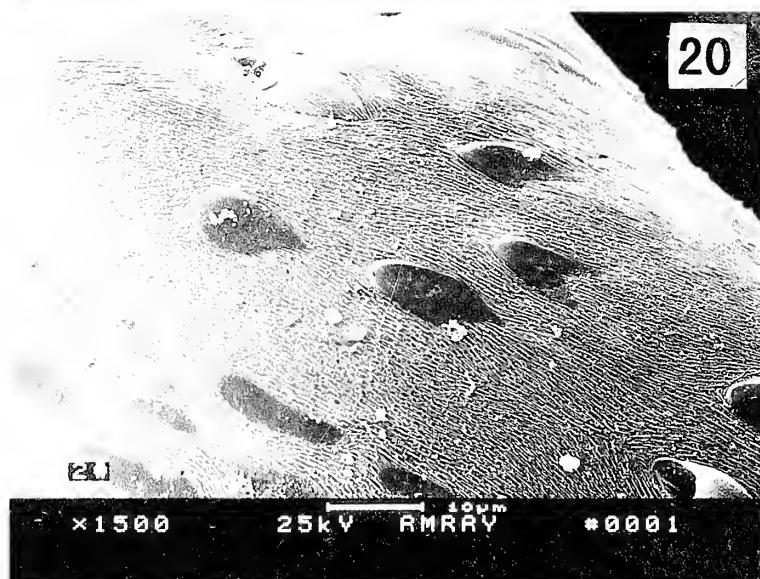
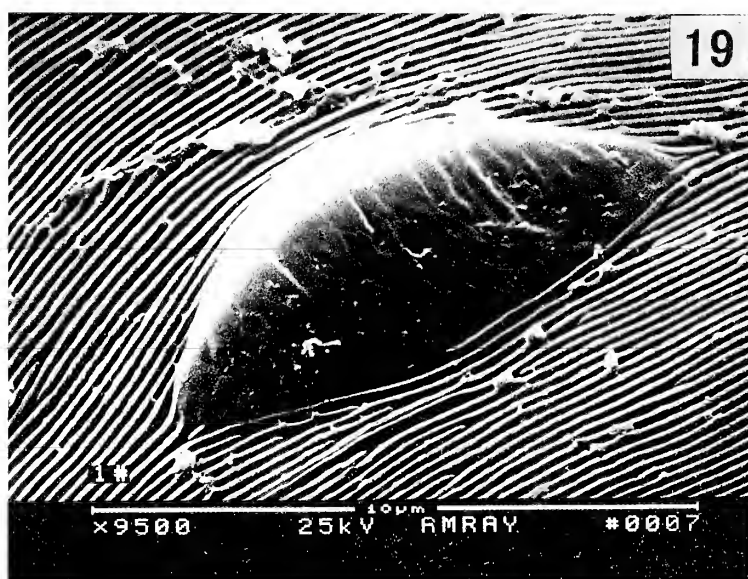
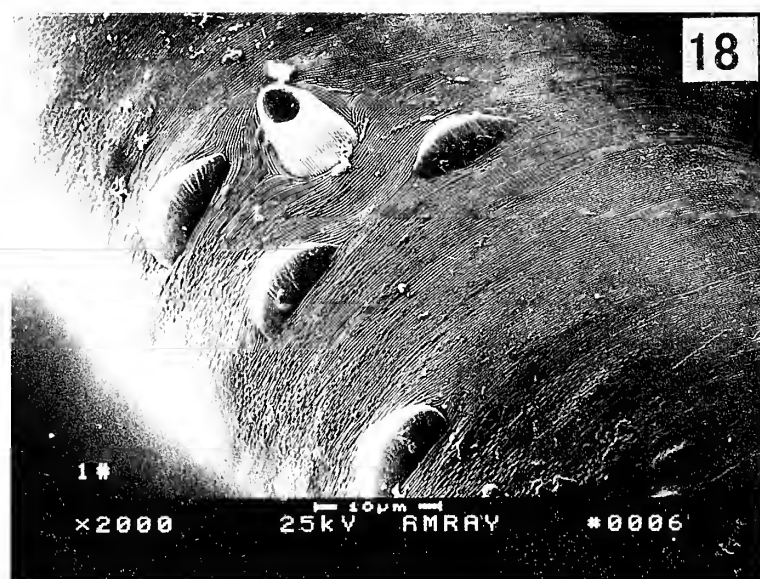
Material examined.—Holotype male, Hui-Sun Experimental Forest Station, Nantou County, Taiwan, April 1998, Sheng-Hai Wu (NMNS-THU-Ar-990043).

Diagnosis.—The new species resembles *Leptoneta taeguensis* Paik 1985 in the shape of the male palpal organ, but differs by the carapace and abdomen having black patches (Fig. 10), which are lacking in *L. taeguensis*; chelicera with 5 retromarginal teeth (Fig. 11), instead of 3 as in *L. taeguensis*; palpal tibia with a large spine and a horn-shaped projection on the distal end, instead of tubercle seen in *L. taeguensis*; and the different shape of laminae of the palpal bulb (Figs. 12, 13).

Description.—Male (holotype): Total length 1.57. Cephalothorax 0.68 long, 0.65

wide; abdomen 0.91 long, 0.56 wide. Carapace yellow. Clypeus 0.14 high, light yellow brown, slightly sloped anteriorly. Thorax black brown on both sides. Fovea brown. Six eyes: ALE: PLE: PME (0.08: 0.07: 0.07); ALE–PME 0.08, PLE–PME 0.02, PLE–PLE 0.09. Chelicera light yellow brown, with 7 promarginal teeth and 5 retromarginal teeth. Endite, labium and sternum deep yellow. Legs light yellow brown, with several slender spines. Measurements of palp and legs: palp 1.11 (0.45, 0.18, 0.23, –, 0.25); I (2.12, 2.65, lost, 2.00, 1.18); II (1.40, lost, lost, lost, lost); III (1.13, lost, lost, lost, lost); IV (1.58, lost, lost, lost, lost). Abdomen elliptical, scattered with thin white hairs, dorsum black-brown, with several yellow patches, venter and spinnerets light yellow. Palpal femur and tibia without thick long spines dorsally; tibia with 2 distal projections on outer side, 1 spine-shaped, the other horn-shaped; cymbium not branched (Figs. 12, 13).

Female: Unknown.



Figures 18–23.—Cuticular plates of tibial and patellar glands. 18–19. Cuticular tibial plate of *Leptoneta changlini* new species; 20–21. Cuticular patellar plate of *Leptoneta taiwanensis* new species; 22. Cuticular tibial plate of *Leptoneta huisunica* new species; 23. Cuticular patellar plate of *Leptoneta nigrabdomina* new species.

Etymology.—The specific name refers to the black abdomen of the holotype.

Leptoneta taiwanensis new species

Figs. 14–17, 20, 21

Material examined.—Holotype male, Hui-Sun Experimental Forest Station, Nantou

County, Taiwan, February 1998, Hai-Yin Wu (NMNS-THU-Ar-990044).

Diagnosis.—This species is similar to *Leptoneta monodactyla* Yin, Wang & Wang 1984 in the shape of the palpal organ, but can be easily distinguished by the male palpal tibia which has a spine-shaped projection on the

distal end rather than finger-shaped as in *L. monodactyla* (Figs. 16, 17); cymbium branched near the distal end with a triangular laminar spur on the outer side of the base. In *L. monodactyla* (Fig. 17) the cymbium is unbranched, the laminar spur is lacking and the palpal laminae are shaped differently (Figs. 16–17).

Description.—Male (holotype): Total length 1.56. Cephalothorax 0.68 long, 0.66 wide; abdomen 0.90 long, 0.61 wide. Carapace yellow, with light yellow brown radial furrows and cervical grooves. Fovea short, light brown. Clypeus 0.18 high, distinctly sloped anteriorly. Six eyes: ALE: PLE: PME (0.05: 0.03: 0.03); ALE–PME 0.07, PLE–PME 0.04, PLE–PLE 0.05. Chelicera light orange, with 8 teeth on promargin and 5 on retromargin. Endites and labium light yellow brown. Sternum yellow. Legs yellow, with several long and thin spines. Measurement of palp and legs: palp 1.56 (0.65, 0.25, 0.27, –, 0.39); I (1.99, lost, lost, lost, lost); II (1.51, lost, lost, lost, lost); III (1.22, lost, lost, lost, lost); IV (1.68, lost, lost, lost, lost). Abdomen oval, dorsum yellow, with indistinct light yellow brown patches, venter yellow, with a light yellow brown rectangular patch behind the epigastric fold. Femur and tibia of palp without thick spines dorsally, tibia with a spine-shaped projection on outer side of distal end (Figs. 16–17). Cymbium of palpal organ with two branches on the distal end (Fig. 17).

Female: Unknown.

Etymology.—The specific name is a noun in apposition referring to Taiwan.

TIBIAL AND PATELLAR PLATE MORPHOLOGY

In this study the tibial or patellar cuticular plates of each of the new Taiwanese species of *Leptoneta* were examined by SEM. *Leptoneta changlini* and *L. huisunica* have similar plates on the patellae and tibiae. Because the tibiae of *L. nigrabdomina* and *L. taiwanensis* were not available, only the patellae of these two species were examined. The tibial and patellar plates of *L. huisunica* (Fig. 22) and patellar plates of *L. nigrabdomina* (Fig. 23) and *L. taiwanensis* (Figs. 20, 21) are paramecium shaped and resemble those of the *Leptoneta* species from the Mediterranean region (see Platnick 1986, figs. 17–20). The tibial plates of *L. changlini* (Figs. 18, 19) resemble the pa-

tellar plates of *Archoleptoneta stridulans* Platnick 1994 (see Platnick 1994, fig. 8) in shape, but the former is hunched in the center and thus *L. changlini* is unlikely to be a member of this genus. Only two southeast Asian leptonetid genera have previously been studied using an SEM: *Masirana akiyoshiensis* (Oi 1958) lacks tibial or patellar plates, and the tibial plate of *Falcileptoneta striata* (Oi 1952) is round, bearing a large, longitudinal median ridge (Platnick 1986). Since the tibial plates of *L. changlini* are so unique, perhaps this species should be placed in a novel genus. Because a detailed survey of the tibial or patellar plates of southeast Asian leptonetids is currently not available, it seems sensible to let the problem lie until more work is undertaken.

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REPRODUCTIVE BIOLOGY OF URUGUAYAN THERAPHOSIDS (ARANEAE, MYGALOMORPHAE)

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ABSTRACT. We describe the reproductive biology of seven theraphosid species from Uruguay. Species under study include the Ischnocolinae *Oligoxystre argentinense* and the Theraphosinae *Acanthoscurria suina*, *Eupalaestrus weijenberghi*, *Grammostola iheringi*, *G. mollicoma*, *Homeomma uruguayense* and *Plesiopelma longisternale*. Sexual activity periods were estimated from the occurrence of walking adult males. Sperm induction was described from laboratory studies. Courtship and mating were also described from both field and laboratory observations. Oviposition and egg sac care were studied in the field and laboratory. Two complete cycles including female molting and copulation, egg sac construction and emergence of juveniles were reported for the first time in *E. weijenberghi* and *O. argentinense*. The life span of adults was studied and the whole life span was estimated up to 30 years in female *G. mollicoma*, which seems to be a record for spiders. A comprehensive review of literature on theraphosid reproductive biology was undertaken. In the discussion, we consider the lengthy and costly sperm induction, the widespread display by body vibrations of courting males, multiple mating strategies of both sexes and the absence of sexual cannibalism.

Keywords: Uruguayan tarantulas, sexual behavior, sperm induction, life span

Theraphosids are the largest and longest-lived spiders of the world. Despite this, and the early contributions of Petrunkevitch (1911, 1934) and Baerg (1928, 1958), their biology remains poorly known. However, more and more research is currently being carried out. A thorough understanding of theraphosid biology and ecology is necessary from a conservation standpoint because natural populations may be threatened by habitat disturbances and captures for pet commerce. An understanding of theraphosid reproduction is necessary to facilitate captive breeding and to reduce pressures on wild populations. Although the neotropical region is the most speciose in theraphosids, most studies are restricted to a few nearctic species. Phylogenetic systematics of neotropical Theraphosinae was recently analyzed (Pérez-Miles et al. 1996; Bertani 2000; Pérez-Miles 2000) facilitating identification for biological studies and evolutionary interpretation. The reproductive biology of some Uruguayan theraphosids has previously been described by Costa & Pérez-Miles (1992), Pérez-Miles & Costa (1992),

Pérez-Miles et al. (1993), Pérez-Miles et al. (1999) and Costa et al. (2000).

In this paper we report on seven species of theraphosids studied in the field and laboratory during more than 20 years. These species include a wide range of sizes from the small *Homeomma uruguayense* (Mello-Leitão 1946) to the large *Grammostola* spp. During this time, we accumulated a diverse and rich store of information on these different species. This comparative study is discussed through a comprehensive review of the literature on Theraphosidae.

METHODS

Species studied.—The only Ischnocolinae studied was *Oligoxystre argentinense* (Mello-Leitão 1941). It is a small to medium sized theraphosid (Table 1) living in rocky hills throughout Uruguay. The other species studied belong to the Theraphosinae. *Grammostola mollicoma* (Ausserer 1875) is a large-sized species generally living under stones and occasionally in burrows, in hilly zones of Uruguay. Two geographical forms of this species are recognized by color differences and

Table 1.—Carapace length (in mm) of the seven species studied. *G. mollicoma* includes both northern and southern forms.

Species	Females			Males		
	Mean	SD	N	Mean	SD	N
<i>G. inheringi</i>	28.75	1.50	4	26.25	1.77	2
<i>G. mollicoma</i>	20.17	2.47	20	18.14	1.76	20
<i>P. longisternale</i>	10.76	0.87	3	7.57	0.40	3
<i>E. weijenberghi</i>	9.97	1.20	12	10.28	0.88	12
<i>A. suina</i>	9.80	1.70	13	9.23	0.70	12
<i>O. argentinense</i>	7.81	0.97	7	6.42	0.51	5
<i>H. uruguayense</i>	7.13	0.62	4	6.65	0.82	2

also by slight behavioral differences: one form, called “northern”, is found above the parallel 33°S and the “southern form” is found below this parallel. Because these forms copulate freely with each other in laboratory conditions, their taxonomic status is uncertain. *Grammostola iheringi* (Keyserling 1891) is also a large-sized species; in Uruguay its distribution is restricted to “Quebrada de los Cuervos”, Treinta y Tres. This species does not copulate with either of the *G. mollicoma* forms in laboratory conditions. *Eupalaestrus weijenberghi* (Thorell 1894) is a medium-sized theraphosid living in burrows in meadows throughout the country. *Acanthoscurria suina* Pocock 1903 is medium-sized and lives in both meadows and rocky hills but is distributed only in the southern half of the country. *Plesiopelma longisternale* (Schiapelli & Gerschman 1942) is a medium-sized tarantula that lives throughout the country, and its ecology is similar to that of *A. suina*. Finally, *H.*

uruguayense is a small-sized tarantula, living under buried stones, on hills throughout Uruguay.

Laboratory breeding.—Small specimens were raised in glass jars of 7.5 cm diameter and large specimens were raised in plastic cages with 14 x 20 cm bases. All containers had a substrate of soil or sand, and water provision. They were fed *ad libitum* mainly with cockroaches (*Blaptica* sp.), adult beetles (*Diloboderus* sp.) and *Tenebrio* sp. larvae, according to the size of the spider. Monthly temperature variation in the laboratory is shown in Fig. 1. Behaviors were studied by direct observation and registered by notes and sometimes with photographs. Most observations of sexual behavior were made with the spiders housed in glass containers (base dimensions, 30 x 15 cm).

Field collections and observations.—Field work occurred from 1978–2000. Intensive observations were made between 1987–1990 in hilly zones (Sierra de las Animas, Maldonado, and Quebrada de los Cuervos, Treinta y Tres) and between 1997–2000 in meadows throughout the country. More than 10,000 km were surveyed recording all theraphosids in routes, roads and neighboring fields. Tarantulas were collected mainly by hand but also pit-fall traps (20 cm in diameter) were used several times. About 1000 specimens were recorded, observed or collected, mainly *A. suina* and *E. weijenberghi*. Field observations of sexual behavior were done mainly in the evening and sometimes recorded on video tape and with photographs.

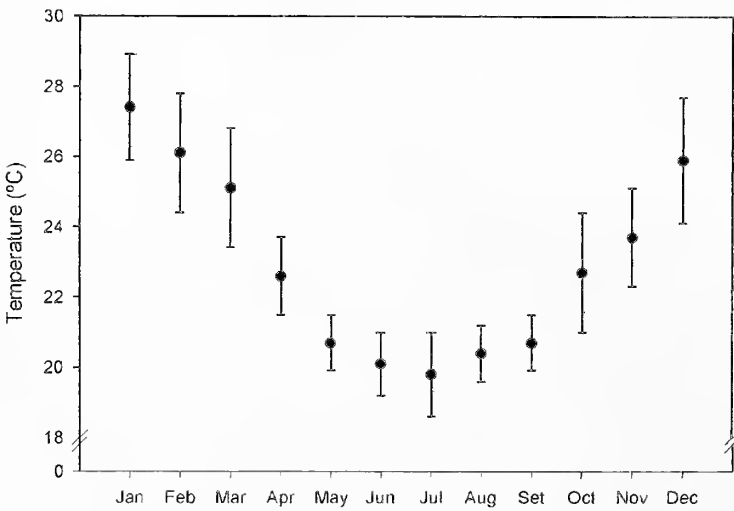
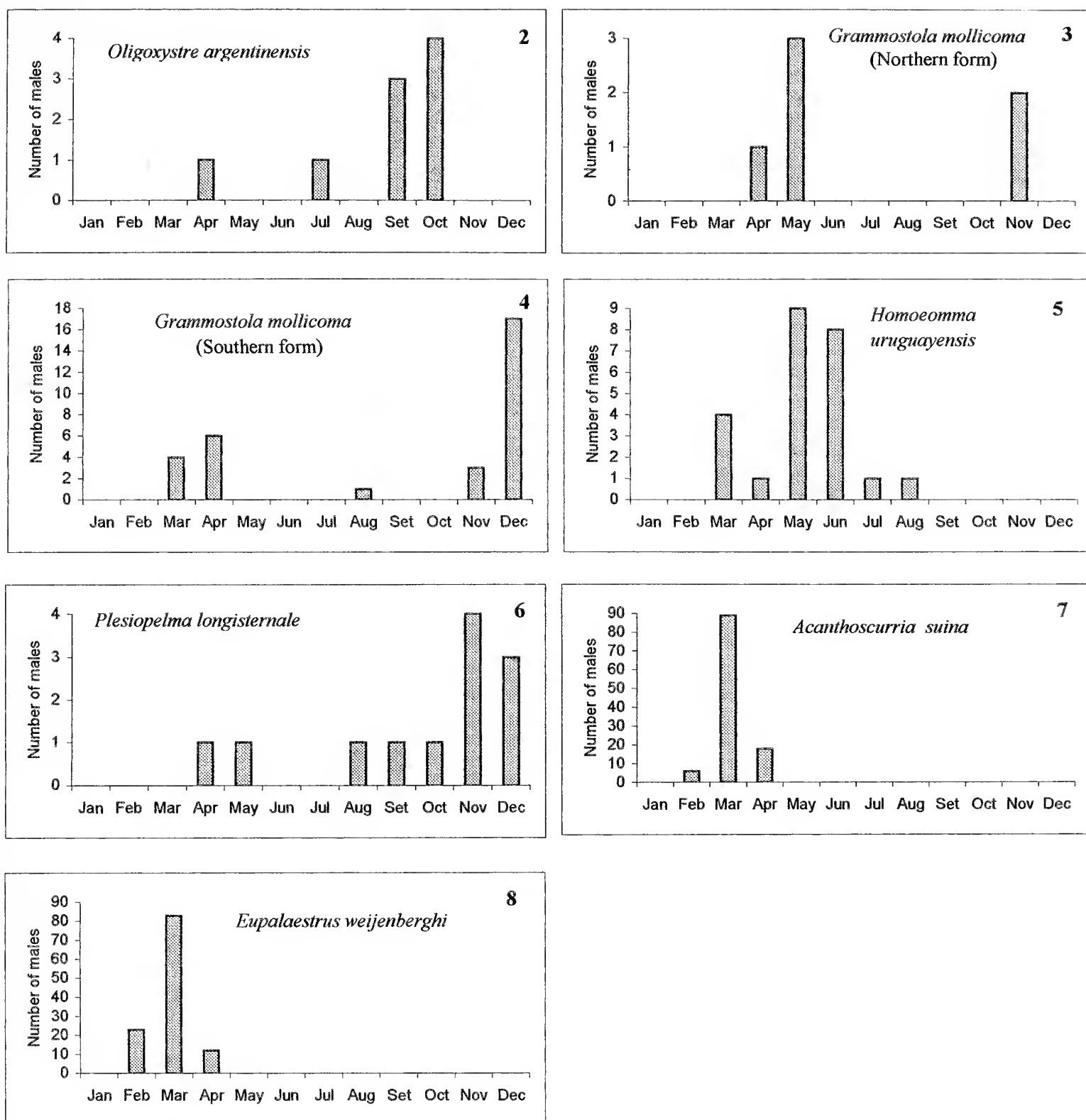


Figure 1.—Room temperature conditions of breeding. Monthly mean and standard deviation were calculated from daily variations during last three years.

RESULTS

Sexual periods.—Sexual activity periods were estimated through the presence of living



Figures 2–8.—Occurrence of adult theraphosid males in the field along the year. *G. iheringi* was omitted because only two males were found in October.

mature males in the field during the study period (Figs. 2–8). Nine males of *O. argentinense* were collected from April to October. In *G. mollicoma* (southern form), 31 males were collected in autumn and spring with a clear peak in December. In the northern form six males were collected with a similar distribution. Two males of *G. iheringi* were collected in October. Twelve males of *P. longisternale* were collected from April to December. Twenty-four males of *H. uruguayense* were collected in autumn and winter. One hundred eighteen males of *E. weijenberghi*

were collected from the end of February to April. One hundred thirteen males of *A. suina* showed a similar pattern of occurrence.

Sperm induction.—In general terms, sperm induction in Theraphosidae is characterized by the construction of a large and dense sperm web attached to the container walls and usually inclined with respect to the soil. Considering mainly laboratory observations in *G. mollicoma* (southern form) and *E. weijenberghi*, the main behavioral sequence of sperm induction is represented in Fig. 9. Males dig a shallow depression removing soil

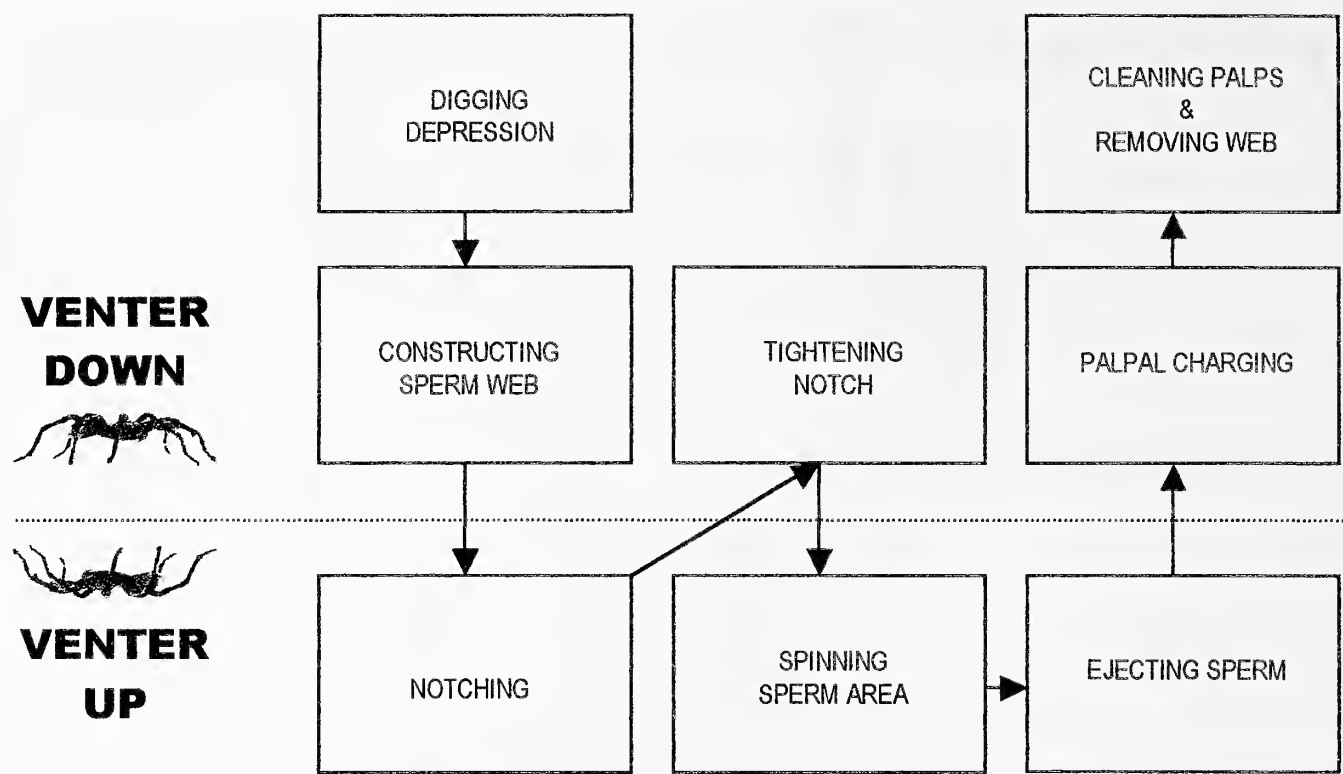


Figure 9.—Diagrammatic representation of a general sequence of behaviors during sperm induction (see text).

adhered to silk threads. The sperm web is constructed over the course of a few hours. With its ventral surface towards the web, the male moves under the sperm web producing a notch in an edge and separating the sperm web from the substrate. Then this web remains hanging up, loose and fixed by the other edges. Later the male moves from under the web and climbs on it to pull the web on a side tightening the notch. This notch is semicircular and clearly delimited (Fig. 10). The male moves beneath the sperm web again, with the venter upward, spinning, especially in an area close to the notch. Apparently the male orients himself placing coxae IV hairs against the notch edge and consequently the genital opening is placed under the reinforced area of the web where he deposits a sperm droplet. During this deposition the prosoma remains out of the web. Then the male gets out and stands on the web with the venter oriented downward, searches for the web edge and seeks the droplet with the palps. Once found, the male starts alternate rapid palpal movements contacting the tip of the palpal bulb with the droplet (palpal charging). The embolus has an angle of approximately 90° with the palpal tibia during sperm charge. Afterwards, the male cleans his palps with the mouth parts and usually pulls out the web and eats it.

The main characteristics of sperm induction are given in Table 2. In one case of *G. mol-*

licoma (southern form) we observed a sperm induction in detail. During sperm web construction, the spinnerets contacts had a frequency of 54 per minute. Web size was 12 cm in length by 8 cm in width and one edge was fixed to the cage wall 4.5 cm above the soil. The male spent 13.5 min spinning the sperm area. Then he took the sperm deposition position and rubbed the genital area against the web alternating with palpal grooming movements, this maneuver took 30.2 min. The sperm droplet deposition was performed in less than 2 min. The male spent 4.3 min to locate the sperm droplet. Palpal charging was done mainly by movement of the patella-tibia joint; distal segments of palps oscillated alternately forward-and-backward. Each palp initially oscillated at 190 times per minute, this increased to 220 and then decreased slowly to 170 (at 24 °C). The whole charging period took around 2 h (end not observed). Finally the male removed and ate the web.

In northern populations of *G. mollicoma*, only one sperm induction was observed in July. One male *G. iheringi* molted to adult on 6 March and made his first sperm induction 10 d later. Two males of this species were observed building sperm webs: 5 h and 2 d before sperm deposition, respectively. In the small-sized *H. uruguayense*, one male made a sperm web 15.6 mm wide. He remained under the web for more than an hour and deposited

10



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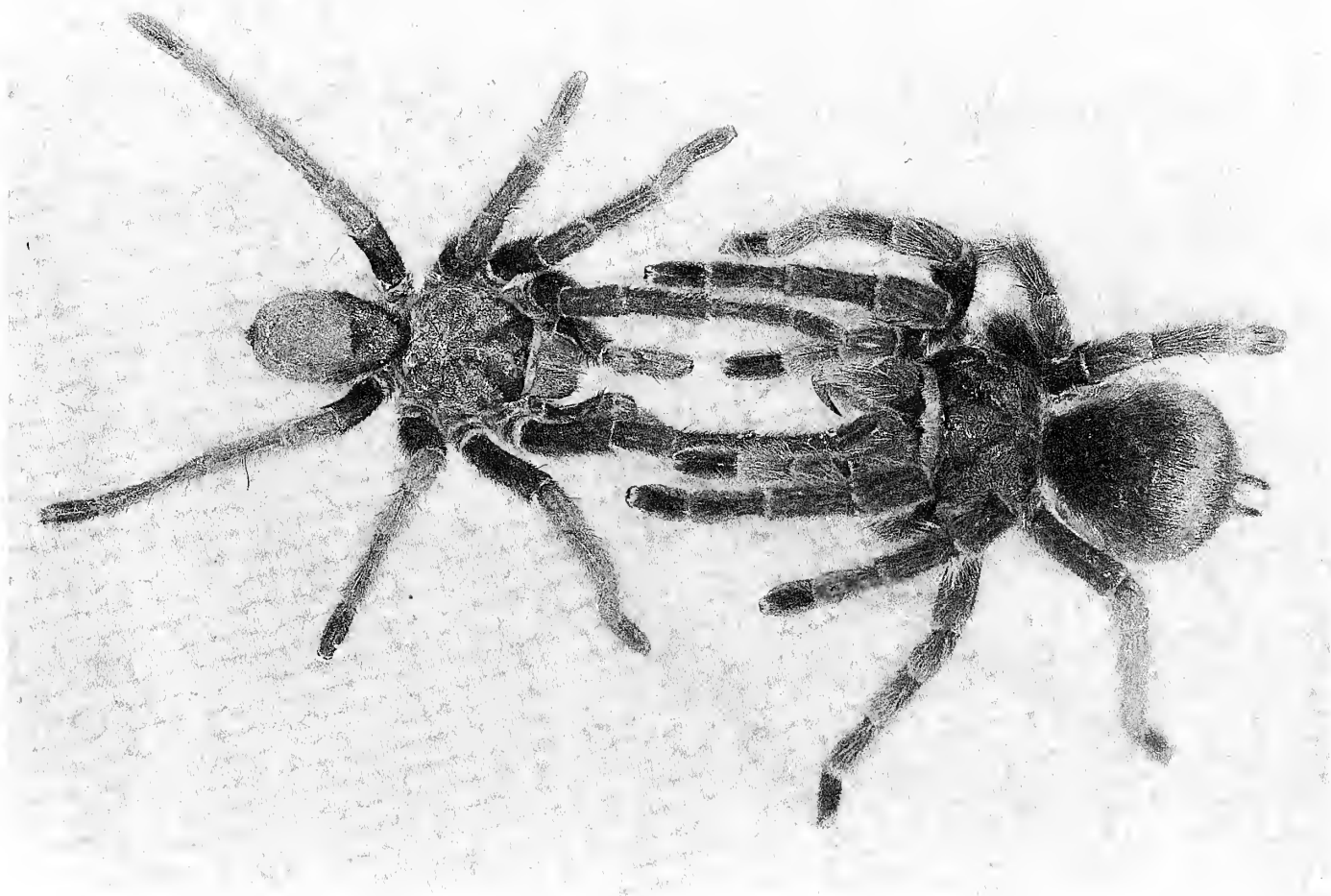


Figure 10.—Male of *E. weijenberghi* before sperm deposition. See the notched edge of sperm web.
Figure 11.—Male (at left) of *G. mollicoma* (Southern form) extending his forelegs and taps the female.

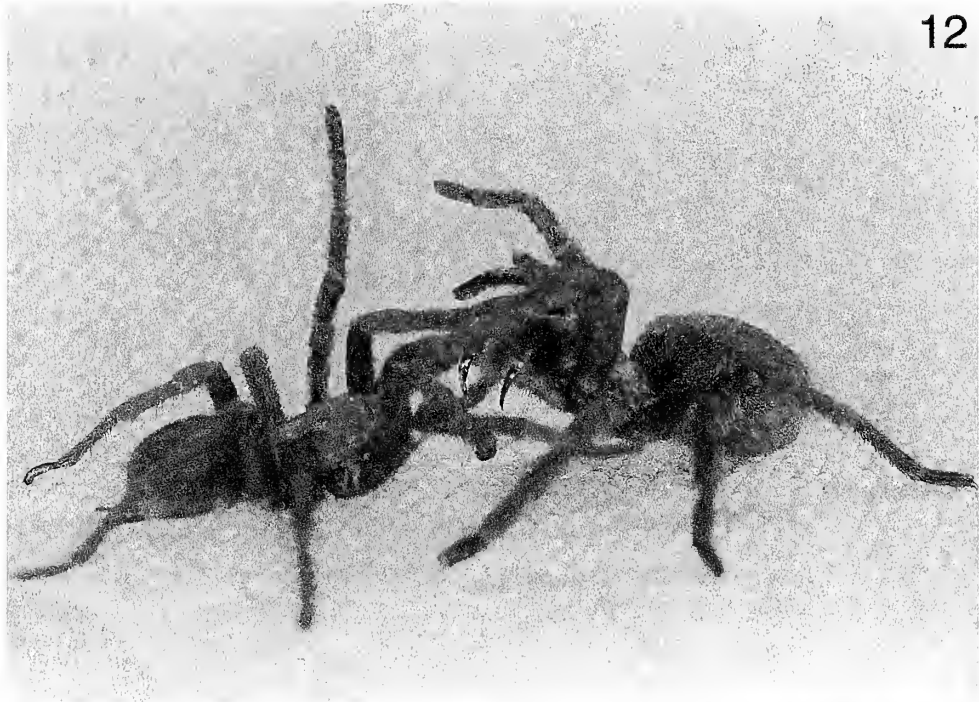


Figure 12.—Male (at left) of *G. mollicoma* (Northern form) trying to clasp open fangs of female. Male left leg II is raised to beat female.
Figures 13–14.—Male of *G. iheringi* clamping female fangs and advances downward with palps alternate movements which contact female venter; 12. Lateral view (male at left); 13. View from the back of the male.

Table 2.—Characteristics of sperm inductions observed in laboratory conditions. (– = No data).

Species	Months (and number) of observation	Duration of sperm web construction (h)	Duration of spinning + sperm depositions (min)	Duration of palpal charging (min)	Frequency of palpal charging (one palp) (per min)	Occurrence of sperm web removal
<i>G. iheringi</i>	Mar (1), Apr (1), Jun (1), Sep (1), Oct (2)	5 2	30 19	102 36	146 132	Yes
<i>G. mollicoma</i> Southern form	Mar (2), May (2), Jul (2), Sep (1), Dec (1)	3.3	45.7	120	170 to 220	Yes
<i>P. longisternale</i>	Aug (1), Nov (1)	—	19.4	108	141	Yes
<i>E. weijenberghi</i>	Mar (10), Apr (2), May (4)	—	—	30 55	52 94	Yes
<i>A. suina</i>	Mar (7), Apr (4), May (1), Jun (1)	—	—	98	135 121	Yes
<i>H. uruguayense</i>	Apr (1), May (1)	—	20	100 124	138 94	Yes
<i>O. argentinense</i>	Feb (1), Mar (1), Apr (4), May (2), Jun (1), Jul (1), Ago (6), Oct (2), Nov (1)	2.1	1.3 to 20	52.3 ± 15.7 <i>n</i> = 7	127.4 ± 24.0 <i>n</i> = 7	Yes

a sperm droplet of 3 x 1 mm. Palpal movements had an amplitude of 1 mm; when the embolous contacted the droplet, palpal organ tips were separated by approximately 1.5 mm.

Two sperm webs of *E. weijenberghi* were found in abandoned burrows in the field together with tarantula exuviae; one sperm web was found on 29 February and the other on 14 March. Two males of *E. weijenberghi* and two of *A. suina* performed 4 sperm inductions each during two months, in the laboratory. During sperm deposition in males of *O. argentinense* we observed lateral abdominal movements similar to those performed when spinning; in one case a frequency of 26 movements per minute was observed. The sperm droplet was oval (2.5 x 1 mm).

Courtship and Mating.—With the exception of *H. uruguayense*, we observed male courtship behavior in all species after contact with female silk but before direct contact with her in both the field and the laboratory. Courtship generally included: body vibration caused by leg III movements, palpal drumming, tapping the female with extended forelegs (Fig.11), male body movement downward and male pushing female (Fig. 12), female threat-like behavior (raising the carapace and open-

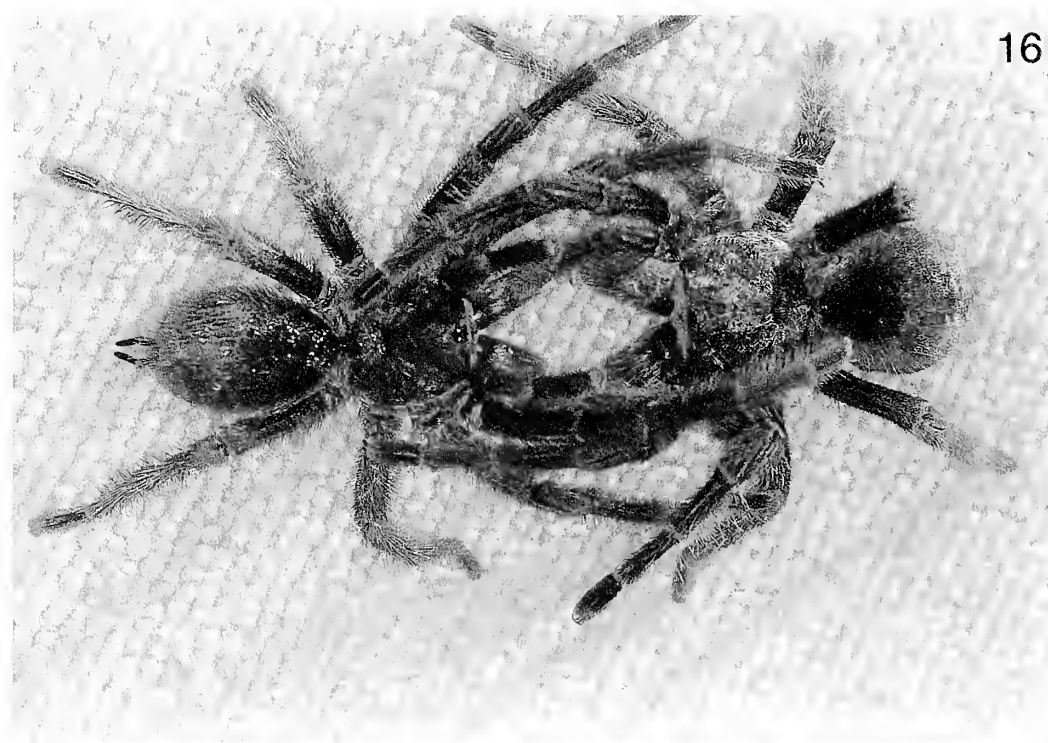
ing fangs), and clasping female's open fangs with male tibial apophysis (Figs. 13, 14). Then the male pushed the female, raising her and extending his palps (Fig. 15). At this moment we generally observed alternate palpal movements which contacted the female on her venter. Females arched backwards (dorsal flexion) up to an angle of 90° between carapace and abdomen. The usual sequence of events was: male body vibrations, tapping with extended forelegs, male pushing and clasping female fangs. Palpal insertions were few, brief and alternate; also copulation duration was brief (see below). At the end of the copulation, the males vibrated, tapped the females with forelegs, and unclasped. Males usually then walked away or, more rarely, re-initiated courtship and mating.

Species-typical behaviors, as they differ among the species, are shown in Table 3. In the field, courted females of *E. weijenberghi* displayed foreleg dorsal-ventral rapid movements at the entrance of their burrows. Males of *E. weijenberghi* and *A. suina* courted at the burrow entrance and partially penetrated the burrow, keeping the hind legs out. Then body vibration, palpal drumming, and leg tapping behaviors attracted the females, and mating

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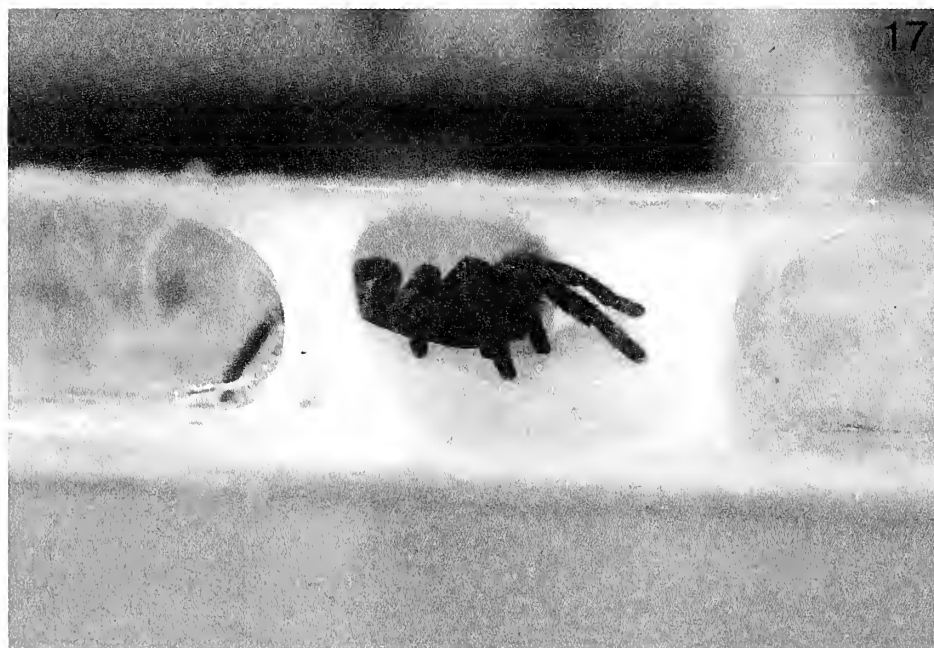


Figure 15.—Copulatory position in *G. mollicoma* (Northern form): male (at left) extending his palps.

Figure 16.—*G. iheringi* couple showing an aggressive postcopulatory behavior (male at left). This display seems to be rare in theraphosids.

Figure 17.—*O. argentinense* female in her nest with the fixed egg sac below her. Petri dish was cut to facilitate vision.

Table 3.—Courtship and mating behaviors which showed qualitative interspecific differences (see text).

Species	Phero- mone recogni- tion	Female leg display	Leg II beating	Female threat-like behavior	Palpal touching female venter	Female dorsal flexion	Posmat- ing threaten- ing display
<i>G. iheringi</i>	Yes	No	Yes	Yes	Intense	Yes	Yes
<i>G. mollicoma</i>							
Southern form	Yes	No	Yes	Yes	Yes	Yes	No
Northern form	Yes	No	Yes	Yes	Yes	Yes	No
<i>P. longisternale</i>	Yes	No	No	Yes	Yes	Yes	No
<i>E. weijenberghi</i>	Yes	Yes	No	Yes, but inconspicuous	Yes	Pronounced	No
<i>A. suina</i>	Yes	No	No	Yes	Yes	Pronounced	No
<i>H. uruguayense</i>	?	No	No	Yes	Yes	Pronounced	No
<i>O. argentinense</i>	Yes	No	No	Yes	Yes	Yes	No

took place at the burrow entrance. In the laboratory, *Grammostola* spp. and *P. longisternale* copulated in an open arena (without a burrow) but in the other species, couples frequently lost their equilibrium when mating in this condition. In *Grammostola* spp. courtship, a singular behavior was observed: the male beat spasmodically with legs II on the female's legs; these movements could be alternate or synchronous with both legs. In this genus the most frequent sequence was body vibration, legs II beating, and pushing female. Beating was also observed during unclasp- ing. The number of insertions, insertion duration and copulation duration of the species studied are given in Table 4.

No sexual cannibalism was observed. In *G. iheringi* a ritualized display was usual when unclasp- ing which involved both partners face to face, with open fangs contacting each other (Fig. 16). After that the males moved away,

and no injuries were produced in these inter- actions.

Egg sacs.—Egg sacs of *P. longisternale* were observed in the field in December and January (two egg sacs examined in the labo- ratory contained 103 and 111 eggs). In *G. mollicoma* (southern form) five egg sacs were observed: one on 14 December (288 eggs), two in January (one of 4.8 x 3.9 x 2.0 cm, 199 spiderlings in fourth and fifth stages ac- cording to Galiano 1969), two in February and one in early March (137 spiderlings in fourth stage according to Galiano 1969) in the field. Two other females were observed in their retreats in the field with emerged spider- lings in February and March. In the labora- tory, the egg sac construction in *G. iheringi* (23 April, 28 November, 8 and 30 December) was characterized by the complete covering of the inner walls of the plastic cage (23 x 14 x 10 cm) by dense web, as described by Mel-

Table 4.—Copulation duration, number of insertions and insertion duration in the species studied. *Cop- ulation interrupted by loss of equilibrium; **one copulation interrupted by female rejection; —no data.

Species	Copulation duration (minutes)			Number of Insertions			Insertion duration (seconds)		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
<i>G. mollicoma</i> S	16.7	15.8	4	16.3	4.3	4	19.6	2.3	2
<i>G. mollicoma</i> N	3.8	1.1	7	6.6	5.0	7	16.6	3.1	3
<i>G. iheringi</i>	6.1	5.1	3	5.3	2.3	3	18.8	6.7	2
<i>A. suina</i>	—	—	—	2.0	—	1*	—	—	—
<i>E. weijenberghi</i>	0.5	0.1	2**	2.0	0	2	—	—	—
<i>P. longisternale</i>	5.3	2.1	6	4.2	0.8	6	—	—	—
<i>H. uruguayense</i>	>0.7	—	6*	1.3	0.5	4*	—	—	—
<i>O. argentinense</i>	0.4	0.1	2	3.0	1.4	2	—	—	—

Table 5.—Mature lifespan of males.

Species	Captured as adults (in months)			Complete (in months)	
	Mean	SD	n	X	n
<i>G. mollicoma S</i>	33.3	7.4	4	48	1
<i>G. mollicoma N</i>	29.1	17.3	4	36	1
<i>G. iheringi</i>	—	—	—	45.6	1
<i>A. suina</i>	3.9	1.2	21	6.8	1
<i>E. weijenberghi</i>	6.1	1.1	19	8.7	1
<i>P. longisternale</i>	—	—	—	19	1
<i>H. uruguayense</i>	3	—	1	4.1	1
<i>O. argentinense</i>	4.5	0.3	2	13.5; 11.1	2

chers (1964) in *Pamphobeteus nigricolor* (Ausserer 1875). Three *A. suina* made egg sacs in the laboratory on 6 & 8 December and 29 September; they were eaten on 5 January, 29 December and 30 September, respectively.

A complete cycle: female molting—copulation—egg sac construction and spiderling emergence in *E. weijenberghi* was observed in a laboratory container with soil and a burrow. Molting took place on 8 December, copulation on 20 July, egg sac construction on 14 November and spiderling emergence on 27 January. We estimated there were more than 100 spiderlings. Egg sac care by the female involved the positioning of the egg sac in the entrance of the burrow, maintaining it under her body. When spiderlings emerged she partially plugged the burrow entrance with silk, soil and egg sac remains. The spiderlings moved away from the container on 14 February. The female molted again on 4 March. In the field we found empty egg sacs near burrow entrances on 15 & 27 February, and two cases on 7 March. The last of these egg sacs contained 541 chorions and two sizes of exuviae. A female with an egg sac containing spiderlings was observed on 27 February. Two other *E. weijenberghi* made egg sacs in the laboratory in November and on 8 December, and were eaten on 17 & 29 December, respectively.

O. argentinense (three observations in the laboratory, in petri dishes) made egg sacs during November. Females constructed silk tubes with dense walls of 3.5–4 cm in length and 3 cm in diameter. The egg sacs were flattened, discoid (1.2 cm in diameter) and remained fixed inside the tube wall (Fig. 17). Two egg sacs were fixed vertically and one was fixed horizontally. Females remained close to the

egg sacs. One of the females reached maturity in the laboratory, mated and made a viable egg sac: spiderlings emerged 37–41 d after oviposition. Neonates were pale yellow, but molted immediately becoming light brown. Seventy-one spiderlings were counted from this egg sac. The other female ate the egg sac on 4 December.

Egg sacs made in the laboratory were generally eaten or abandoned with the exception of one case in *P. longisternale* reported by Costa & Pérez-Miles (1992), one case in *E. weijenberghi* and another in *O. argentinense* (this paper).

Lifespan.—Theraphosid males have a shorter lifespan than females and do not molt when adults. Most males were captured as adults and only part of their adult life was recorded; some males molted to maturity in the laboratory and the whole adult lifespan was recorded (Table 5).

Considering the extremely long lifespan of theraphosid females, very few data were recorded in the laboratory and most were taken from individuals captured as adults. In the smallest sized *H. uruguayense* a female lived more than 11 y and molted 5 times in this period while a female of *P. longisternale* lived more than 4 y. In *G. mollicoma* (southern form) three females lived more than 12, 16 & 20 y as adults. Two females reared since neonate stage, reach adulthood at 9 & 13 y. Consequently, based on laboratory results, we estimate the maximum lifespan of *G. mollicoma* to be about 30 y. Molting frequency of adult females was measured in the laboratory: two females of *H. uruguayense* molted every 2 y; one *P. longisternale* molted every 1.5 y; one *G. iheringii* molted every 2 y; five *G. mollicoma* (northern form) molted every 2 y, and

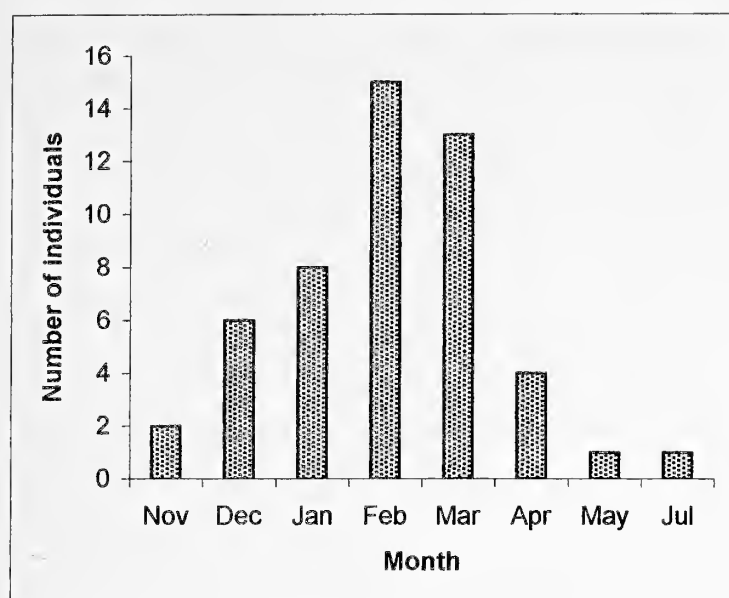


Figure 18.—Annual distribution of molts in adult females of *G. mollicoma* (southern form).

16 of the southern form molted every 2.3 ± 0.9 (range 1–5) y. In *G. iheringi*, *G. mollicoma*, *P. longisternale*, *H. uruguayense* and *E. weijenberghi* adult molts took place mostly in February and March. One adult female of *E. weijenberghi* molted five times during 7 y. Females of *A. suina* molted annually, during the summer. In *G. mollicoma* (southern form) annual molting distribution is shown in Fig. 18. One adult female of *O. argentinense* molted yearly during the summer, during 3 y.

DISCUSSION

Reproductive activities in these theraphosids of the temperate region coincide with seasonal changes. *Eupalaestrus weijenberghi* and *A. suina* showed a restricted sexual period of only 2 mon in late summer and early autumn. In Arkansas (in a similar latitude to Uruguay, but in the Northern Hemisphere) Baerg (1958) reported the sexual period for northern tarantulas (*Aphonopelma* spp.) in the summer. In desert conditions, Prentice (1997) found two clear breeding seasons for *Aphonopelma* spp.: fall and summer; Punzo & Henderson (1999) reported a summer sexual period for *A. hentzi* (Girard 1852). In an arid area of Australia, males of *Selenocosmia stirlingi* Hogg 1901 probably reach maturity in summer (Kotzman 1990). In Uruguay, most species showed a wider period of sexual activity, which was reduced in colder and warmer months. The exceptional sexual activity period of *H. uruguayense* in cool-cold season (autumn and winter) could be interpreted as an ecological strategy to avoid predation due to its small

size, as suggested by Pérez-Miles et al. (1993). Coincidentally, another very small, sometimes sympatric mygalomorph spider, the mecicobothriid *Mecicobothrium thorelli* Holmberg 1882, also has a similar sexual period (Pérez-Miles et al. 1993; Costa & Pérez-Miles 1998).

Seasonal mass movements of males is a widespread phenomenon in tarantulas usually related to weather conditions and sexual activity. It also has been interpreted as a form of migration by some authors (Baerg 1958; Magnusson 1985) due to the coordinated movements of the spiders. We did not observe coordination in male mass movements in Uruguayan tarantulas which was in agreement with observations of Janowsky-Bell & Horner (1999) in *A. hentzi*.

The restricted sexual period of *A. suina* and *E. weijenberghi*, together with the high frequency of “walking males” could be related to the ecological pattern of these species. They live in open fields (meadows) and no refuges are known for adult males, while females live permanently in burrows. The “walking males”, concentrated in time and space, may reflect a strategy for saturation of predators occurring in this season. Also the co-occurrence of these species could reinforce the saturation of predators. The brief life-span of adult males (only 2 mon in nature) is artificially increased in laboratory conditions, but is also lower in comparison with the other Uruguayan tarantulas. Consequently, the sperm storage period in the field is always extended (at least 8 mon), considering that egg sac production takes place in December. Baerg (1958) reported that in *Aphonopelma* spp. the sperm remains stored for 10 mon (August–June in the northern hemisphere).

It is usually expected that males of large-sized species have a longer life-span than that of small-sized species. For example the small *H. uruguayense* lives 3–4 mon while large *Grammostola* spp. live around 30–45 mon. *E. weijenberghi* and *A. suina* males are exceptions to this, because they are relatively large-sized and have a very reduced life-span. This fact is probably related to their habitat: the other long-lived species occupy hilly zones with major availability of cryptozoic refuges. These ecological characteristics could also explain the prolonged sexual periods in *Gram-*

mostola spp., *P. longisternale*, and *O. argentinense*.

Sperm induction.—The large size of the sperm mat of theraphosids compared to Araneomorphae, involves a substantial cost in time and effort by these spiders. The behavioral sequence observed in sperm induction agrees in general terms with the accurate description of Petrunkevitch (1911) in *A. hentzi*. This author reported that the sperm droplet is placed “on top of the web” and palps were charged through the sperm web but Petrunkevitch (1934) observed that the sperm droplet is placed hanging from the underside of the sperm web in *Cyrtopholis jamaicola* Strand 1908. This last observation agrees with Gerhardt (1929, 1933), Baerg (1958), and with our observations. Male behavior involving coxae IV to “select” the exact site to place the sperm droplet agrees with the observation of Petrunkevitch (1934) in *C. jamaicola*.

The construction of a reinforced area in the sperm web (where the droplet is deposited) was also reported for theraphosids by Petrunkevitch (1911), Baerg (1928), Gerhardt (1929) and Melchers (1964). Probably this area has specialized silk that prevents the droplet from diffusing into the rest of the web. Gerhardt (1929) in *Avicularia avicularia* (Linnaeus 1758), Petrunkevitch (1934) in *Cyrtopholis jamaicola*, and Melchers (1964) in three theraphosid species, reported the presence of an adhesive substance deposited from the genital pore on the web before the sperm droplet deposition. Melchers (1964) also described glandular organs probably responsible for this secretion (epigastric glands: Lopez, 1987). We did not observe any similar substance in the species studied but our observations were made without magnification.

The sperm droplet was oval in all species studied and the spiders were oriented perpendicular to the major axis of the droplet during charge. This could facilitate the lateral contact of the palpal organs.

Theraphosid males spend a long time in sperm induction in comparison to other spiders (Gerhardt 1929). Males of species that live in rocky environments showed higher sperm charge durations in comparison with *E. weijenberghi* that live strictly in open fields. In the latter species the short duration of sperm charge could be related to the scarcity of protected sites for this conspicuous event.

Petrunkevitch (1911) indicated that papal charging duration was more than an hour in *A. hentzi* and in 1934 indicated 90 minutes for *C. jamaicola*; Gerhardt (1929) reported 40–128 min in *A. avicularia* and Melchers (1964) 90 min in *P. nigricolor*. Minch (1979) reported a sperm induction duration of 23–85 min in *Aphonopelma chalcodes* Chamberlin 1940. In *E. weijenberghi*, a higher frequency of palpal movements during sperm charge could be expected to compensate for the short duration, but that was not the case. The total number of palpal organ contacts with the droplet was 3,000–10,000, similar to *O. argentinense* (10,000) but fewer than *G. mollicoma* southern form (45,000). The number of contacts estimated from Petrunkevitch (1911) in *D. hentzi*, by Gerhardt (1929) in *A. avicularia*, by Petrunkevitch (1934) in *C. jamaicola*, by Baerg (1928, 1958) in *Aphonopelma* spp., by Melchers (1964) in *P. nigricolor* and by Minch (1979) in *A. chalcodes* are within the range of Uruguayan species assuming these authors counted movements of only one palp.

Sperm induction was very frequent in the laboratory, with the same male recharging his palpal organs several times (a record of more than 17 sperm inductions in six weeks was reported by Baerg 1958). This could be interpreted in two ways: (1) the sperm charged during one sperm induction is not enough to inseminate several females (sex ratio is biased toward females in adults) or, (2) there is some selective pressure to avoid old sperm in the palps. The first sperm induction is performed early by males after maturation: Minch (1979) observed one male of *A. chalcodes* that made his first sperm induction 10 d after maturity as we observed in *G. iheringi*. Baerg (1958) also indicated that males of *A. hentzi* performed their first inductions 3–15 d after maturation, in the field. Prentice (1997) reported the first sperm inductions of males of *Aphonopelma* spp. 3–21 d after maturity. This author also observed first sperm induction in *A. joshua* inside the burrow if it is sufficiently wide in any region, as we observed in *E. weijenberghi*. Gerhardt (1929) reported the first sperm induction in *A. avicularia* 28 d after maturity.

The sperm web destruction observed in Uruguayan species was also reported by Gerhardt (1929) in *A. avicularia*, by Petrunkevitch (1934) in *C. jamaicola*, by Baerg (1958)

in *Aphonopelma* spp., by Melchers (1964) in *P. nigricolor* and by Minch (1979) in *A. chalcodes*.

Courtship and mating.—Chemical sexual communication in theraphosids was suspected by Baerg (1958) and observed by Minch (1979), Prentice (1997), Shillington & Verrell (1997), Yañez et al. (1999), thereby discrediting previous hypotheses about the absence of chemical cues in these spiders (Petrunkévitch 1911; Baerg 1928; Platnick 1971). Our results agree with the existence of female contact sex pheromone. The exception in *H. uruguayense* could be attributed to the low number of observations or to the absence of female silk in the laboratory recipients. Obviously, pheromones on female silk facilitates the sexual encounter and species recognition.

Body vibrations caused by leg III movements were observed in all Uruguayan theraphosids and were also described for *A. chalcodes* (Minch 1979) and in Mecicobothriidae (Costa & Pérez-Miles 1998). Prentice (1997) described body vibrations in *Aphonopelma* spp. including audible stridulation in *A. joshua*. Similar behavior (quiver/shaking) has also been described in *A. avicularia* (Gerhardt 1929) and *Aphonopelma* spp. (Shillington & Verrell 1997; Punzo & Henderson 1999). Considering that mecicobothriids + microstigmatids are the sister group of the rest of Tuberculotae (a clade that includes theraphosids) (Raven 1985), an early acquisition of this behavior is suggested. Body vibrations (shaking) were also described for *Brachypelma klaasi* (Schmidt & Krause 1994) by Yañez et al. (1999). The possible function of this behavior is distant seismic communication. Also body vibrations in the entrance of the burrow could generate air waves of low frequency. This behavior causes females of *A. suina* and *E. weijenberghi* to emerge from the retreat, whereas in *A. chalcodes* females emerge due to male tapping with front legs (Minch 1979).

Palpal drumming is a widespread behavior in the Theraphosidae (Costa & Pérez-Miles 1992; Minch 1979; Stradling 1994; Shillington & Verrell 1997; Punzo & Henderson 1999; Yañez et al. 1999) and could involve acoustic/vibratory signals just as body vibrations could. Tapping movements with the forelegs on the substrate are frequent in *Aphonopelma* spp. (Baerg 1958; Prentice 1997; Shillington & Verrell 1997), but we

only observed this behavior in *A. suina* and *E. weijenberghi*, suggesting its function as a communication mechanism is mainly useful for burrowing spiders.

Tapping movements (leg fencing) with male forelegs on the female cause the female to assume a threat posture with open fangs as was observed by Petrunkévitch (1911) in *D. hentzi*, Gerhardt (1929) in *A. avicularia*, Baerg (1958), Minch (1979), Shillington & Verrell (1997) and Punzo & Henderson (1999) in *Aphonopelma* spp. This female "aggressive" display is a necessary condition for the male to clasp (Gerhardt 1929 in *Phormictopus cancerides* (Latreille 1806)). As is well known for theraphosids, all the species studied here have specialized tibial apophyses to clasp female chelicerae and improve male security during copulation. This clasping also supports the female so the male can reach the genital area. In *E. weijenberghi* we observed an active female display with foreleg and palpal movements, which possibly orients the male in the open field at a relatively short distance. This female "courtship" behavior is unusual in theraphosids and could involve the generation of airborne vibrations.

The male spasmodic beating with legs II was unique to *Grammostola* and could be a synapomorphy for this genus. Its function could be the relaxation of female fangs, taking into account that it is mainly displayed during clasping and unclasping.

In *A. avicularia*, females live in arboreal silken retreats and copulation takes place outside the retreat (Stradling 1994). In the species living in burrows, copulation always takes place at the entrance (Costa & Pérez-Miles 1992; Shillington & Verrell 1997; Yañez et al. 1999). This location for mating is probably due to space limitations in the female's burrow; it also avoids the risk to the male of being closed into the burrow. The predation risk of the couple in an exposed mating site is minimized by the brief copulation duration (lasting only a few minutes), which was also reported for other theraphosids (Gerhardt 1929; Baerg 1958; Minch 1979; Stradling 1994; Huber 1998; Punzo & Henderson 1999). In summary, in all species studied a low number of brief insertions was recorded. Differences in the number of insertions and copulation duration between the southern and northern form

of *G. mollicoma* may help clarify the taxonomic status of these forms.

In theraphosid spiders it is difficult to establish which palpal organ (left or right) penetrates in which female spermathecal gonopore (left or right), because female gonopores are placed in a common atrium which opens into the epigastric furrow. Additionally, observation is made difficult by the brief copulation, the position, and the very hairy features. Despite the description of ipsilateral insertion (right in right, left in left; Minch 1979), an indiscriminate insertion pattern was found in *O. argentinense* using monopalpectomized males (Costa et al. 2000).

The passivity and relaxed condition of the female is probably maintained by male palpal touches on the female venter during copulation, a similar behavior (palpal boxing) was described by Petrunkevitch (1911) in *D. hentzi*, by Brazil & Vellard (1926) for *Grammostola* spp., by Gerhardt (1929) for *A. avicularia* and by Yañez et al. (1999) for *B. klaasi*.

The frequent loss of equilibrium during copulation in most species studied (with the exception of *Grammostola* spp. and *P. longisternale*) could be related to their adaptation to mate strictly in the entrance of burrows; females maintain part of the body inside the burrow. The male pushes the female backward and she leans part of her body on the soil and burrow wall. The extreme case of female dorsal flexion was observed in *E. weijenberghi* where copulation probably cannot occur in the open field; a similar flexion was reported in other species living in burrows (Petrunkevitch 1911; Baerg 1958). Female dorsal flexion was also reported in *A. avicularia* and *P. cancerides* by Gerhardt (1929).

Brazil & Vellard (1926) reported sexual cannibalism in some Neotropical theraphosids with the exception of *G. longimana*. Bücherl (1952) reported the "massacre" of males caused by females in 14 of 15 species of theraphosids studied. He explained it as a first maternal (nutritional) action. Based on this, Lourenço (1978) expected a sex ratio biased in favor of males in *A. atrox*. Punzo & Henderson (1999) found 20% sexual cannibalism during courtship of *A. hentzi* in staged encounters. Despite this, we observed no sexual cannibalism in the field or laboratory. From our results, and according to Petrunkevitch (1911), Gerhardt (1929), Baerg (1958), Minch

(1979), Stradling (1994), Shillington & Verrell (1997) and Prentice (1997) the absence of sexual cannibalism seems to be the rule for theraphosids. However, occasionally we observed a female of *A. suina* eating a conspecific male in the burrow entrance. Celerier (1981) studying the Eumenophorinae *Scodra griseipes* Pocock 1897 (now *Stromatopelma*) reported that in 83 attempts 13 males were eaten. However, rare postcopulatory female attacks were reported in *A. iodium* by Prentice (1997), Shillington & Verrell (1997) in *Aphonopelma* sp., and in *B. klaasi* by Yañez et al. (1999). Males and females probably reach adulthood with a 1:1 sex ratio but in nature the sex ratio is strongly biased in favor of females because of their longer lifespan. For this reason males are expected to have evolved efficient defenses against sexual cannibalism, mainly because males probably copulate several times in their lives (Buskirk et al. 1984). Baerg (1958) reported one male *Aphonopelma* spp. copulated 12 times in captivity and estimated a sex ratio of 1 male to 6 or 7 females, in the summer. Shillington & Verrell (1997) observed that females of *Aphonopelma* sp. copulated 5–7 times. Stradling (1994) reported a male of *A. avicularia* that mated with 5 females. Celerier (1981) stated that one male of *S. griseipes* can copulate with several females. Taking into account the abundance of females, a strong intrasexual competition among males is not expected and we did not observed male–male fighting nor female mate guarding. Male competition could be restricted to finding females as discussed by Shillington & Verrell (1997). A post-copulatory aggressive display observed in males of *G. iheringi* resembles the female-female interactions reported by Pérez-Miles & Costa (1992) and its interpretation remains obscure.

Egg sacs.—*A. avicularia* makes only one egg sac per year in the tropics (Stradling 1994). All species studied apparently produced only one egg sac per year, mainly during the warm period. Baerg (1958) observed egg sac care in the summer in *Aphonopelma* spp. and Prentice (1997) observed it in *A. joshua*. Brazil & Vellard (1926) reported that *G. actaeon* and *G. longimana* molt 2 mon after egg sac production. Coincidentally, Bücherl (1952) reported that females molt after spiderling dispersion. Lourenço (1978) found the

occurrence of egg sacs during a prolonged period in *A. atrox* (spring–summer) in the tropical region. In our study egg sacs were observed in the field mostly in the summer (temperate region).

The period from oviposition to emergence of spiderlings was reported by Stradling (1994) in *A. avicularia* as 51 d, by Celerier (1981) in *S. griseipes* as 52.5 d, by Baerg (1958) in *Aphonopelma* spp as 56 d, by Ibarra-Grasso (1961) in *G. burzaquensis* as more than 50 d, and by Costa & Pérez-Miles (1992) in *P. longisternale* as 49 d. Except for the Ichnocolinae *O. argentinense* with attached egg sac (also reported by Goloboff 1987) all other Uruguayan tarantulas are Theraphosinae and have free cocoons. Attached egg sacs were reported also for a few Old World Harpactirinae and Eumenophorinae (Marshall et al. 1999). More knowledge about the egg sac condition in Theraphosidae may clarify phylogenetic trends. We did not observe the incorporation of urticating hairs into the egg sacs in the studied species as was reported by Melchers (1964) and Marshall & Uetz (1990).

Two complete successful reproductive cycles were reported here in *E. weijenberghi* and *O. argentinense*, both from females that molted in the laboratory. Reproductive success in captivity in theraphosids is unusual and was indicated for the first time by Celerier (1981) in *S. griseipes* and then by Costa & Pérez-Miles (1992) for *P. longisternale*. Usually in theraphosids egg sacs made in the laboratory are eaten or abandoned.

Life span.—The adult life span of male tarantulas under laboratory conditions seems to be an overestimation of what occurs under field conditions. This was clear in *E. weijenberghi* and *A. suina* in which adult life was estimated in the field using pit-fall traps and periodic collection. In these species adult males were recorded in the field mostly in March and April while in the laboratory they live 6 and 4 mon, respectively. As in other spiders, male life-style is very different from juveniles and females; males wander seeking females, incurring a high cost of energy and risks, and they rarely feed. At the end of the breeding season they have lost body mass and their abdomens are very reduced (Janowsky-Bell & Horner 1999).

In the laboratory conditions are the opposite, which could explain their long life. The

long life-span of theraphosids is well known. In the Aviculariinae *A. avicularia* males reach adulthood at 2.5 y living 2–4 mon as adults; females mature in 3 y and can live as long as 7 y, under tropical conditions (Stradling 1978, 1994). Celerier (1981) reported that males of *S. griseipes* live 0.4–0.7 y as adults while females live up to 6 y. Males of this species reach maturity between 1.1 and 1.2 y while females mature between 1.3 and 1.7 y. Baerg (1928, 1958) reported that males of *Aphonopelma* spp. live up to 1 y as adults, reaching maturity in about 10–13 y while females reach maturity in 10–12 y. Also Gerhardt (1929) found that a male of *P. cancerides* lived 1 y in the laboratory. Ibarra-Grasso (1961) reported that *G. burzaquensis* reach adulthood in 6 y and males live 2–4 y as adults while a female lived more than 15 y as an adult. Galiano (1984, 1992) found that males of *Acanthoscurria sternalis* Pocock 1903 reach maturity in 4–6 y and females in 6 y; males live 9 mon–2.5 y as adults while a female lived 9.5 y as adult. Marshall & Uetz (1993) found that in *Theraphosa blondi* (Latreille 1804) both sexes mature in 2.7 y. In *Brachypelma* spp., males live 7 or 8 y to maturity, living less than 1 y as adults, while females live 9–10 y as juveniles and 10 y as adults (Locht et al. 1999). Brazil & Vellard (1926) indicated that males of *G. actaeon* can live up to 18 mon as adults. Millot (1943) recorded a female of *Grammostola* sp. from Uruguay living 12 y as an adult.

Our study confirmed that females of large sized theraphosids can live 30 y in captivity (*G. mollicoma* southern form lived 10 y to maturity and 20 y as an adult). As far as we know, this is a record for life-span in spiders. Stradling (1978) found in *A. avicularia* that adult females molt annually as also indicated by Celerier (1981) for *S. griseipes*. Baerg (1958) found that adult females molt each year or each two years. In agreement with Gerschman & Schiapelli (1950), Ibarra-Grasso (1961) and Prentice (1997), we found that large theraphosids molted about every 2 y, as adults.

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COURTSHIP AND SPERM TRANSFER IN THE WHIP SPIDER *PHRYNUS GERVAISII* (AMBLYPYGI, PHRYNIDAE): A COMPLEMENT TO WEYGOLDT'S 1977 PAPER

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ABSTRACT. The aim of this study was to provide descriptive and quantitative data regarding behaviors involved in courtship and in sperm transfer of the whip spider *Phrynus gervaisii* (Pocock 1894) in order to complete the previous description for this same species given by P. Weygoldt. The specimens were captured in anthills of *Paraponera clavata*, on Barro Colorado Island, Panama. Ten courtship and five sperm transfer sequences were recorded. Four out of five mating sequences with sperm transfer occurred between adults with similar body size and in the other case the female was smaller than the male. Sexual interactions did not occur between very small adults. Two male behavior patterns that have not been reported were observed during the initial stage of courtship: “pedipalp rubbing” and “female operculum rubbing”. Contrary to Weygoldt’s description, in this study the female never performed “shaking” movements with her antenniform legs. It was observed that the two distal horn-like extensions of the spermatophore facilitate the females movements during the sperm transfer. The distal part of the spermatophore stalk provides a suspension area when the female rests on those horns. It was verified that the female can move the claw-like sclerites of the gonopods in all directions. The male executed copulatory courtship and successfully transferred sperm in five analyzed sequences. The female did not pick up the sperm packages when copulatory courtship was not performed. Males that lacked one antenniform leg were able to mate, however they had to perform vibrations more intensely with their non-injured leg for a longer duration. The data are compared with those previously obtained in other whip spiders. Some functional characteristics of the spermatophore and female genitalia of *P. gervaisii* are also discussed.

RESUMEN. El objetivo de este trabajo es aportar datos descriptivos y cuantitativos sobre patrones de comportamiento que ocurren durante el cortejo y transferencia espermática del amblopígido *Phrynus gervaisii* (Pocock 1894) con la finalidad de completar la descripción previa de P. Weygoldt para esta misma especie. Los especímenes fueron capturados en hormigeros de *Paraponera clavata*, en la Isla de Barro Colorado, Panamá. Se registraron 10 secuencias de cortejo y cinco de transferencia espermática. Cuatro de las cinco secuencias de apareamiento con transferencia espermática completa ocurrieron entre adultos de tamaño corporal similar mientras que en el otro caso la hembra fue más pequeña que el macho. No se produjeron interacciones sexuales entre adultos muy pequeños. Durante la etapa inicial del cortejo fueron observados dos patrones de comportamiento masculinos que no habían sido citados con anterioridad: “roces de pedipalpos” y “roces al opérculo genital femenino”. Al contrario de la descripción de Weygoldt, en el presente estudio la hembra nunca realizó movimientos de “latigqueo” con sus patas anteniformes. Se observó que las dos expansiones distales con forma de cuerno del espermatóforo facilitan los movimientos de la hembra durante la transferencia espermática. La parte distal del tallo del espermatóforo ofrece un área de suspensión cuando la hembra se apoya sobre estos cuernos. Se verificó que la hembra puede mover los escleritos en forma de uña de sus gonópodos hacia todas las direcciones. El macho efectuó cortejo copulatorio en cinco secuencias analizadas, en ellas la transferencia espermática fue exitosa. Por el contrario, la hembra no recogió los paquetes espermáticos cuando no existió cortejo copulatorio. Los machos que carecían de una pata anteniforme también fueron capaces de aparear. Sin embargo, ellos tuvieron que realizar más intensamente las vibraciones con sus patas no dañadas, y sobre todo durante un tiempo más prolongado para evitar que la hembra se alejara. Se comparan los datos aquí registrados con aquellos previamente obtenidos en otros amblopígididos. Se discuten algunas características funcionales del espermatóforo y genitalia femenina de *P. gervaisii*.

Keywords: *Phrynus gervaisii*, Amblypygi, courtship, sperm transfer, spermatophore

Whip spiders (Amblypygi) represent an interesting group of arachnids, the biology and natural history of which are still poorly known. Whip spiders have strong, raptorial

pedipalps armed with sharp spines. Since whip spiders continue to molt and grow after reaching sexual maturity, adults of the same species may be different sizes (Weygoldt 1995). The courtship behavior and spermatophore morphology are two of the most fascinating subjects to be analyzed in these animals. Whip spiders use vibration of the "anteniform" first pair of legs during courtship (Thomas & Zeh 1984; Weygoldt 1990). After a prolonged dance, the male turns until facing away from the female and deposits a stalked spermatophore. Then he turns towards the female again and lures her to approach the spermatophore and pick up the spermatozoa (Weygoldt 1990, 1998). Few amblypygid species have been observed (i.e., Weygoldt and others have studied the courtship of 19 out of approximately 125 described species). Although the literature contains general descriptions of the mating, we lack many descriptive and quantitative details of behaviors involved in each stage of the courtship and sperm transfer. In fact, the elaborate displays involved in the courtship and spermatophore deposition of whip spiders show the importance of more detailed observations not only to increase our general knowledge but also to lend insight into the sexual selection that shaped the displays.

Spermatophore morphology and sperm transfer mechanisms vary among genera and families and provide useful characters for systematics (Weygoldt, 1998). One of these families, the Phrynidae, contains medium to large-sized whip spiders and occurs in tropical and semitropical areas of the Americas (Quintero, 1981). The spermatophores of phrynids are large and have triangular, heavily sculptured heads (Weygoldt 1969, 1974, 1977, 1990, 1999). The female genitalia are characterized by the existence of two gonopods, each equipped with a claw-like sclerite that is used to pick up the small sperm packages from the spermatophore (Weygoldt 1990, 1999). It is currently unclear how these claw-like sclerites come into contact with the sperm packages. Similarly, it would be of interest to understand the behaviors, such as copulatory courtship, that occur during and after the sperm transfer. In arachnids copulatory courtship has been observed in spiders (Eberhard 1994), scorpions and solpugids (Peretti 1997, pers. obs.). Although in whip spiders Wey-

goldt (1990, etc.) has mentioned the presence of antenniform tapping along with other male-female contact during the sperm pick-up, it is necessary to add more details to increase our knowledge of this behavior (e.g., do all the males of a same species always perform copulatory courtship?, can any male traits, such as body size, affect copulatory courtship behavior?).

The aim of this study was to provide descriptive and quantitative data regarding behaviors involved in courtship and in sperm transfer of the whip spider *Phrynus gervaisii* (Pocock 1894) in order to complement the previous general description given by Weygoldt (1977) for this species. Weygoldt studied the mating behavior and spermatophore of *Tarantula palmata* Kraepelin 1899, using adults specimens captured in Santa Martha, Colombia. Quintero (1981), in the important revision of the amblypygid genus *Phrynus* in the Americas, synonymized this species with *Phrynus gervaisii*. Thus, in this study Weygoldt's observations are adopted as the most important and direct antecedents, comparing the data with those published by this author and, mainly, adding new details to that general description, in particular with respect to behavioral variation.

METHODS

Capture site and laboratory conditions.—Twenty females and 13 males of *P. gervaisii* were collected in October, 1996 in Barro Colorado Island (Smithsonian Tropical Research Institute -STRI), Panama, where the observations were carried out under laboratory conditions (see details below). The specimens were captured in the morning and in the early afternoon in anthills of *Paraponera clavata* (Hymenoptera, Formicidae) inside the parcel of 50 hectares that STRI has on the island. Externally, these anthills consist of excavations at the base of a tree. *Phrynus gervaisii* lives inside galleries of the anthills, going out at night to feed (Pérez Mendieta 1996; Peretti, pers. obs.). In order to capture specimens I hit the base of a tree containing anthills several times with a metal rod. This made many ants to run out very quickly and made some whips spiders leave the anthills and climb the tree; immediately afterward the specimens were captured (by covering them with plastic containers 9.6 cm in diameter).

The animals were housed individually in cages of different sizes, all furnished with a piece of tree bark set vertically so that they could climb. They were fed crickets and locusts once a week. Moist cotton balls were used to maintain high humidity and the temperature varied from 24–32 °C. Following Weygoldt & Hoffmann (1995), all animals were kept under a light/dark cycle of 12:12 hours. In the present work the dark phase started at 1100 h. This synchronized the activity rhythms of the animals with each other and with our activity.

Analysis of mating and genitalia.—Observations of the mating sequences were made in a 40x30x30 cm mating arena that was furnished with a vertical piece of tree bark from the capture site. The substrate consisted of soil, bark and some stones. All the elements of the arena were replaced with fresh materials prior to each use. A 40 W red lamp allowed observation without disturbance. Oral recordings of 10 mating sequences were made on audio cassettes; seven were described in more detail and five had complete sperm transfer. These matings were always performed using different males and females. The female was introduced first into the arena and 10–15 min later, the male was introduced. Three males lost the distal part of one of their antenniform legs due to the ant attacks observed in the field. These males were useful in determining whether the amputation could affect their ability to perform courtship and sperm transfer. Timing and frequency of behaviors were recorded. Behavior patterns were identified following Martin & Bateson (1993), Weygoldt (1977) and Weygoldt & Hoffmann (1995). In all the specimens prosoma length was used as an index of body size (Quintero 1981).

Every male-female interaction was recorded, with details of the sperm transfer phase. Two matings were interrupted in order to obtain fresh spermatophores still containing spermatozoa. All the spermatophores were preserved in 70% alcohol. One day before and immediately after a mating I observed in a stereomicroscope if the female had sperm under the claw-like sclerites by slightly opening the genital operculum. Approximately eight hours after a complete sperm transfer, three females were sacrificed and dissected to locate spermatozoa in the spermathecae. The contents extracted from each spermatheca were

stained with methylene blue and examined with a light microscope. Genitalia of live and fixed (in alcohol) females were compared and fit with unused spermatophores in order to determine the correspondence among the structures that are closely in contact during the sperm transfer. Finally, each individuals willingness to perform a new mating was observed daily.

One preserved individual has been deposited as a voucher specimen at the Arachnological Scientific Collection of the Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba and one additional specimen was deposited at the Smithsonian Tropical Research Institute, Panama.

RESULTS

Body size and mating.—In the anthills containing individuals of *P. gervaisii* ($n = 28$ of 37 anthills checked) there were one or two adult whip spiders (five cases), but they were never of the same sex. These individuals varied in size, but all of them were sexually mature (e.g., large and small females with offspring were collected). The individuals mated in the lab with others captured in either the same anthill or elsewhere. In all the sequences the female was smaller than the male (Table 1): in four out of five matings with complete sperm transfer the male:female size ratio was 1.08 ± 0.05 (mean \pm SD) and in the other case it was 1.61. The size ratio was 1.04 for another sequence where the female did not pick up the sperm packages. The duration of the courtship was only 9.10 ± 3.10 min when males were smaller than females (size ratio: 0.78 ± 0.20 ; $n = 3$); in two sequences the male moved away first. Sexual interactions did not occur between very small adults (i.e. prosoma length less than 4.3 mm), and in 100% of the trials ($n = 9$) they moved away from each other after a brief contact with their antenniform legs. The mean duration of the complete matings was 3.20 ± 0.73 h; range = 2.22–4.46 h. Males were larger than females (ratio 1.14) in the two shortest matings while the body size ratio was lower in the two longest sequences (Table 1).

Courtship.—This stage represented $92.12 \pm 2.27\%$ (mean \pm SD) of the duration of an average complete mating. In seven out of 10 courtship sequences males remained motion-

Table 1. Main features of seven mating sequences in *Phrynus gervaisii*. Latency is the time from the beginning of the courtship to the onset of the first occurrence of the behavior pattern. Frequency refers to the total number of occurrences of the behavior pattern per mating. (a): the female did not pick up the sperm packages; (b): this sequence was interrupted to obtain a fresh spermatophore.

Sequences	Prosoma length (mm)		Size ratio	Mating duration (h, min)		Grasping with unfolded palps		Female operculum rubbing		Pedipalp rubbing		Spermato-phore deposition		Sperm packages uptaking	
	Male	Female		Latency (min)	Frequency	Latency (min)	Frequency	Latency (min)	Frequency	Latency (min)	Frequency	Latency (h, min)	Latency (h, min)	Latency (h, min)	Copulatory courtship
	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values	Values
1	8.3	8.0	1.03	—	0	—	0	—	0	53.2	1	4h 13'	4h 22'	—	Yes
2	8.8	7.7	1.14	8.6	5	24.5	3	24.5	3	32.3	3	2h 41'	2h 50'	—	Yes
3	8.7	7.6	1.14	13.5	2	18.6	2	18.6	2	29.1	1	1h 57'	2h 8'	—	Yes
4	7.8	7.5	1.04	7	3	—	0	—	0	44.5	1	3h 03'	3h 12'	—	Yes
5	8.8	5.5	1.61	10.3	4	13.2	2	13.2	2	22.4	2	2h 54'	3h 03'	—	Yes
6	8.1	7.7	1.04	5.7	2	34.7	1	34.7	1	45	1	3h 45' (a)	—	—	No
7	7.9	5.6	1.41	4.5	3	—	0	—	0	28.1	1	2h 37' (b)	—	—	—
Mean	8.3	7.1	1.2	8.3	2.7	22.7	1.1	22.7	1.1	36.3	1.4	3h 1'	3h 7'	3h 7'	Presence:
Values	±0.4	±1.1	±0.2	±3.3	±1.5	±9.2	±1.2	±9.2	±1.2	±1.1	±0.8	±45'	±49'	±49'	80%

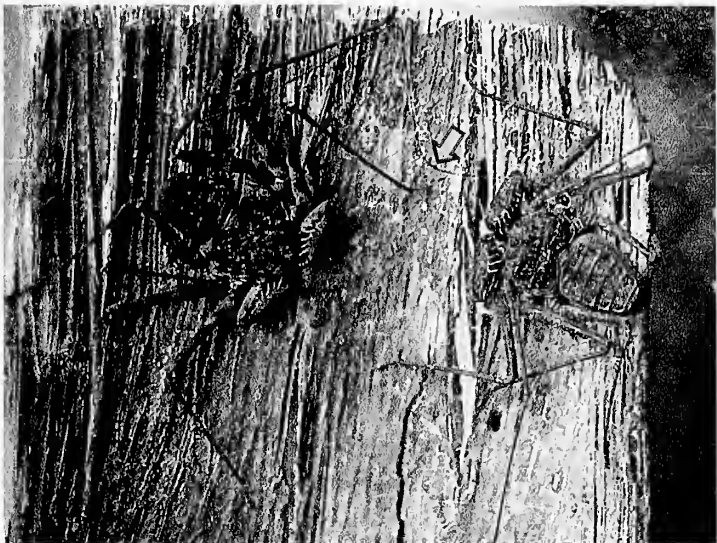


Figure 1.—Courtship in *Phrynus gervaisii*. The male (left) is tapping the females right pedipalp with his left antenniform leg (arrow). This male was able to mate in spite of lacking a part of his right antenniform leg and third leg.

less at the base of a vertical piece of tree bark before the first sexual contact took place. Males and females oriented “face to face” (Fig. 1) and 4.43 ± 1.05 cm apart. In some cases (3 of 10) the female began the contact, approached the male and stayed within one cm of him. As Weygoldt observed, initial “tapping” with the antenniform legs was very light and intermittent. A typical sequence was performed repeatedly (5 ± 2.8 times for courtship, $n = 10$): the male stepped forward, performing tapping and unfolding his pedipalps. Then, the female also did the same sequence (for a more detailed description of each behavior, contact the author).

The male sometimes tried to grasp the female with her unfolded palps (“grasping with unfolded palps”, latency: 8.3 ± 3.3 min) (Table 1). In some sequences (6 of 10) the male performed a behavior that has not been described in either *P. gervaisii* or other whip spiders (“female operculum rubbing”) (Fig. 2). This behavior involves lifting the females caparace and then touching her, from genital operculum to chelicerae, 2–4 times with his palps. The occurrences of “grasping with unfolded palps” and “female operculum rubbing” per mating was higher in the largest males (Table 1).

Contrary to Weygoldt’s observations, in this study the female never performed “shaking” movements with her antenniform legs. After 36.37 ± 10.39 min (from the onset of courtship), staying 8–7 cm from the female, the male emitted an audible sound by rubbing

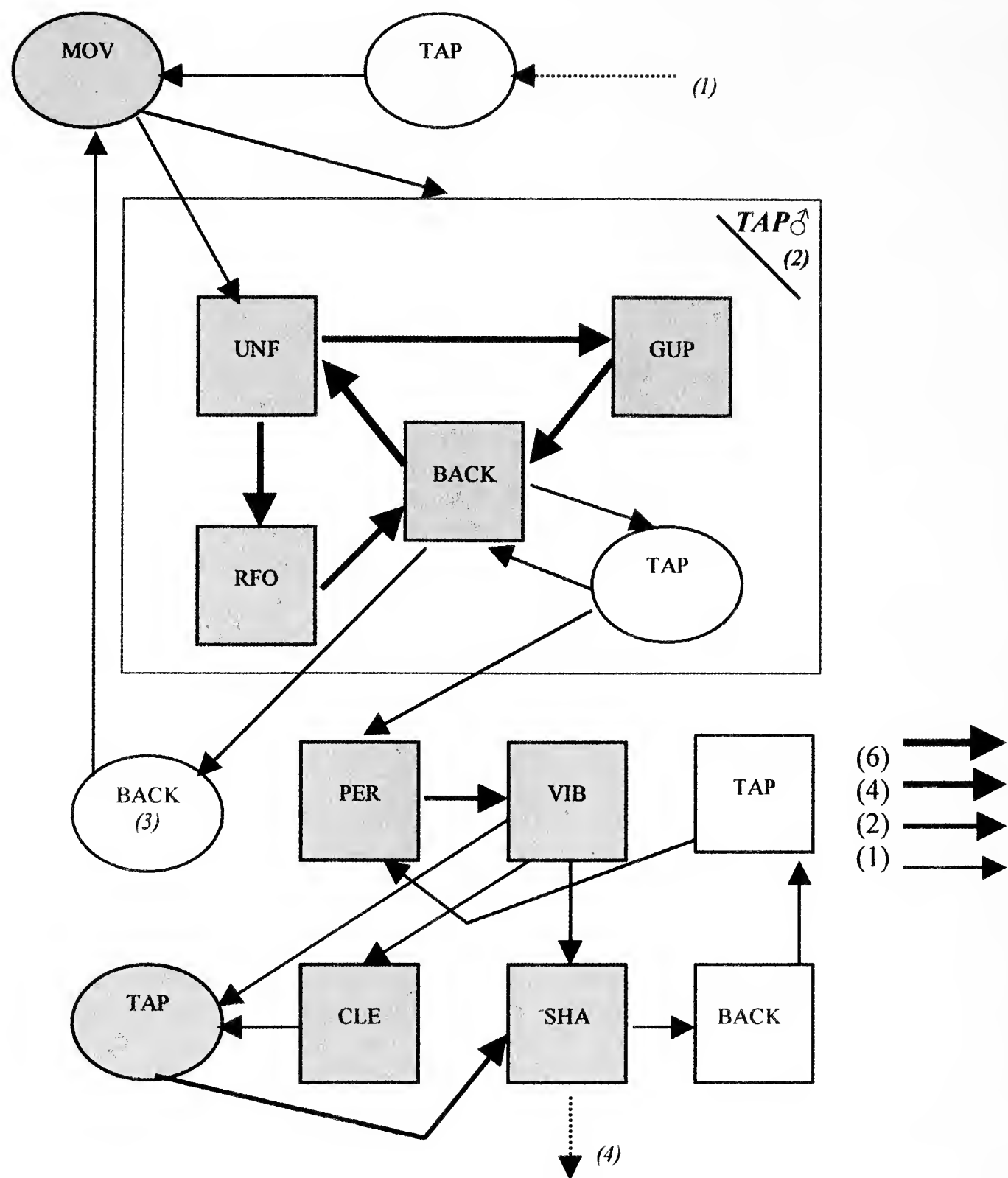


Figure 2.—Flow diagram of a representative courtship sequence in *P. gervaisii*. Each symbol represents a behavior: circles = female, squares = male. The behaviors that happened more than once are shown in gray. Arrows indicate transitions between behaviors. Abbreviations: BACK = backward motion; CLE = antenniform legs cleaning; GUP = grasping with unfolded palps; MOV = forward motion; PER = pedipalp rubbing; RFO = female operculum rubbing; SHA = antenniform legs shaking; TAP = tapping with antenniform legs; UNF = palps unfolding; VIB = antenniform legs vibration. Other references: (1) beginning of the courtship, the female approaches the male and performs TAP; (2) The rectangle includes behaviors that occur while the male executes intense TAP; (3) in this courtship sequence the female moved backwards after a male approached. Thereafter she moved close to the male again; (4) male turning: this represents the beginning of the sperm transfer stage.

the spines of the distal region of his pedipalp tibiae (“pedipalp rubbing”, its frequency of occurrence was higher in the two largest males) (Table 1). This behavior has not been cited before, although Weygoldt (1977) had mentioned sounds like “scrapings”; however

his observations might correspond to what I call “grasping with the unfolded palps”. Then, staying to 3–4 cm in front of the female, the male stepped forward for a last time and performed “tapping” intensively (no vibrations included). Just as described by Wey-

goldt, the male turned until he faced away from the female: this behavior constitutes the beginning of the second stage, the sperm transfer.

Sperm transfer behavior.—During this stage, the male stayed always below the female on the vertical piece of tree bark. As also observed by Weygoldt, approximately ten minutes after turning (10.60 ± 3.30 min, $n = 7$), the male deposited the spermatophore while his antenniform legs crossed each other backwards and vibrated rhythmically (“vibration”) while touching the female. In general, the latency to the “spermatophore deposition” was shorter in the largest males (Table 1). At the end of this behavior, the male did not cross his antenniform legs; and he executed “shaking” 4 or 6 times together with “vibration” (Fig. 3). Weygoldt (1977) reported that the intense movements of the males antenniform legs during the deposition of the spermatophore were similar to those in courtship. Nevertheless in the present study “shaking” was exclusively performed during the deposition of the spermatophore and also when the female approached it. It could be possible that this difference between the studies reflects the difference in the descriptions or perhaps some variability in the sexual behavior because of the male’s sexual receptivity. After turning until facing the female, the male remained over the spermatophore for 8.31 ± 1.01 min ($n = 5$) (“spermatophore protection”), perhaps providing protection for the spermatophore until it hardened. In this study I did not observe the male grabbing the deposited spermatophore as was reported by Weygoldt (1977).

When “vibration” and “shaking” became more vigorous the female moved her antenniform legs forward so that they were touched intermittently by the male’s. The combination vibration-shaking was performed 10–15 times from the beginning of spermatophore protection until the end of the female approach to the spermatophore. Although my description of the female approach to the spermatophore is similar to that of Weygoldt (1977), many details can be added. The female performed gentle movements up and down before picking up the sperm packages. Then, the male increased the intensity and duration of vibration-shaking. Immediately afterwards, she moved over the spermatophore and picked up

the sperm masses (Fig. 3). The dorsal appendages of the spermatophore sloped a little down when the female placed her body over them (Fig. 4). Finally, the female rose and let her body down twice more on the spermatophore before moving away.

Copulatory courtship: The male usually continued vibrating his antenniform legs just as the female took up the sperm packages (Figs. 3–4). During this behavior the males antenniform legs intermittently touched those of the female. In contrast, she neither moved her antenniform legs nor touched the male during this phase (however, before this phase, she did it while the male touched her during the deposition of the spermatophore). Weygoldt (1977) did not mention in his general description that those male vibrating movements occurred again when female picked up the sperm packages. Copulatory courtship was executed in five analyzed sequences, and in all of these the sperm transfer was successful. The female did not pick up the sperm packages in another sequence where no copulatory courtship was performed by the male. Although the copulatory courtship sometimes could include typical movements of “tapping” and “shaking”, these behaviors were more common during the precopulatory courtship.

Post-sperm transfer stage.—After picking up the sperm packages, the female raised her body and ended any contact with the spermatophore (Fig. 3). Weygoldt (1977) did not offer details of this stage. Agonistic behavior did not occur either before or after the separation. In two cases the female moved away first, while the male remained still and then he ate the emptied spermatophore almost completely (the basal part of the stalk remained attached to the soil). In contrast, the female never ate the spermatophore. The ingestion of the post-insemination spermatophore by the male has not been mentioned before for *P. gervaisii*. In species of *Charinus* Simon 1892 the male performed the same behavior whereas in another Phrynidae, *P. marginemaculatus* C. L. Koch 1841, it was the female that ate the empty spermatophore (Weygoldt 1969, 1977, 1990). A male was able to mate again and deposit another spermatophore six days after mating. The females mated again one or two days after mating with the same or a different male.

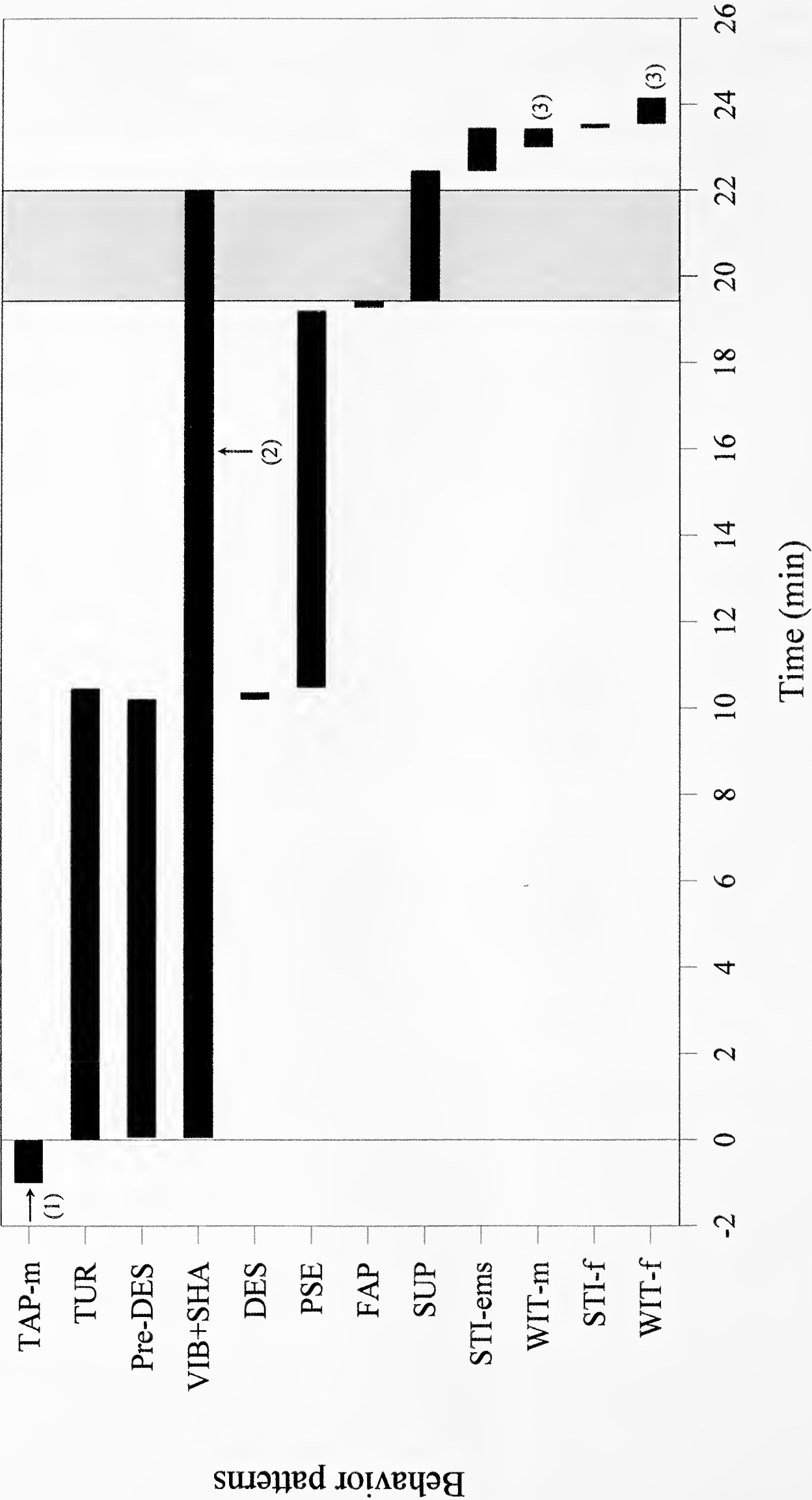


Figure 3.—Diagrammatic chronology of the sperm transfer stage in *P. gervaisii*, beginning with the male “turning” (TUR) (Time = 0), showing the time course of a typical mating sequence. The vertical gray area shows the copulatory courtship stage. Abbreviations: DES = spermatophore deposition; FAP = female approaching to the spermatophore; PSE = spermatophore protection; Pre-DES = preparatory stage for spermatophore deposition; STI-f = female stillness; STI-ems = STI-f over used spermatophore; SUP = sperm packages uptake; TAP-m = male tapping with antenniform legs; TUR = male turning; VIB + SHA = combination of the male behavior patterns “antenniform legs vibration and shaking”; WIT = individual withdrawal (male: m; female: f). Other references: (1) the male was performing TAP before turning; (2) the intensity of the vibrating movements increased. Each ends (3) when either partner is more than 10 cm away from the transfer site.

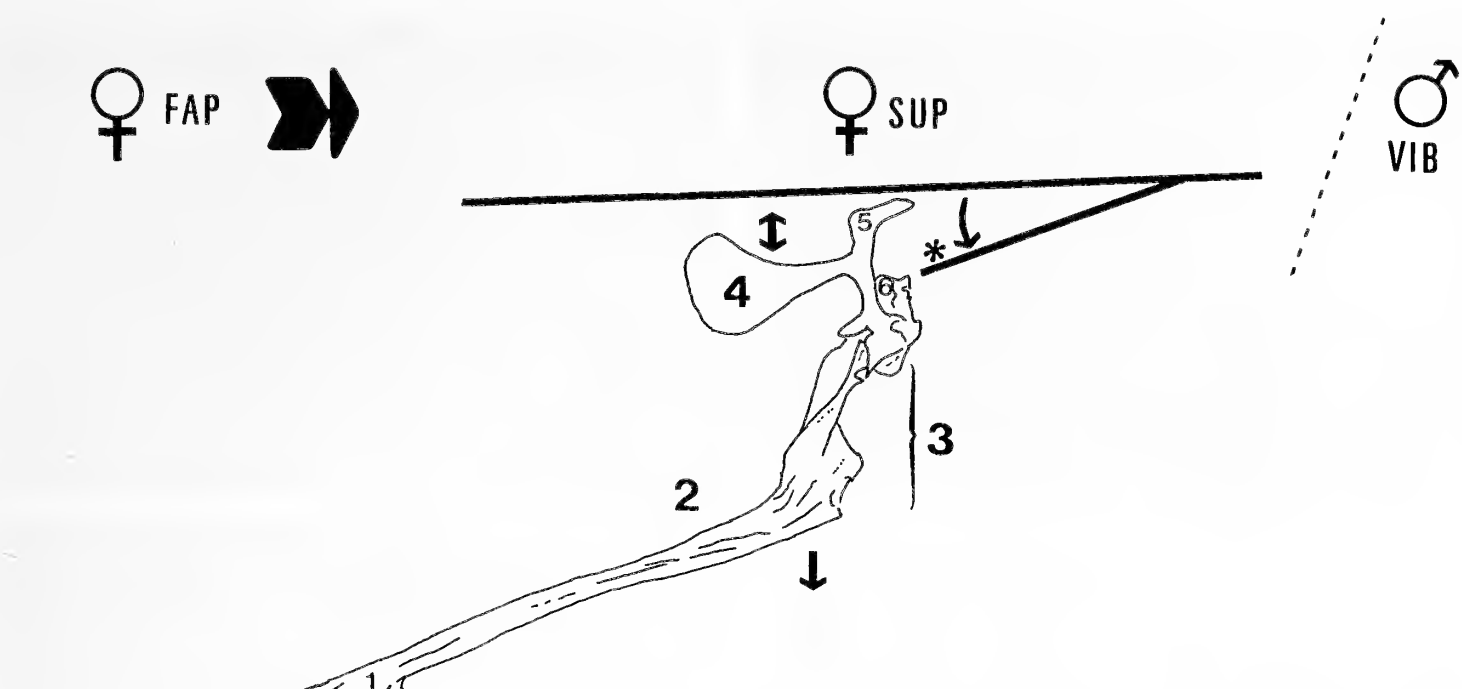


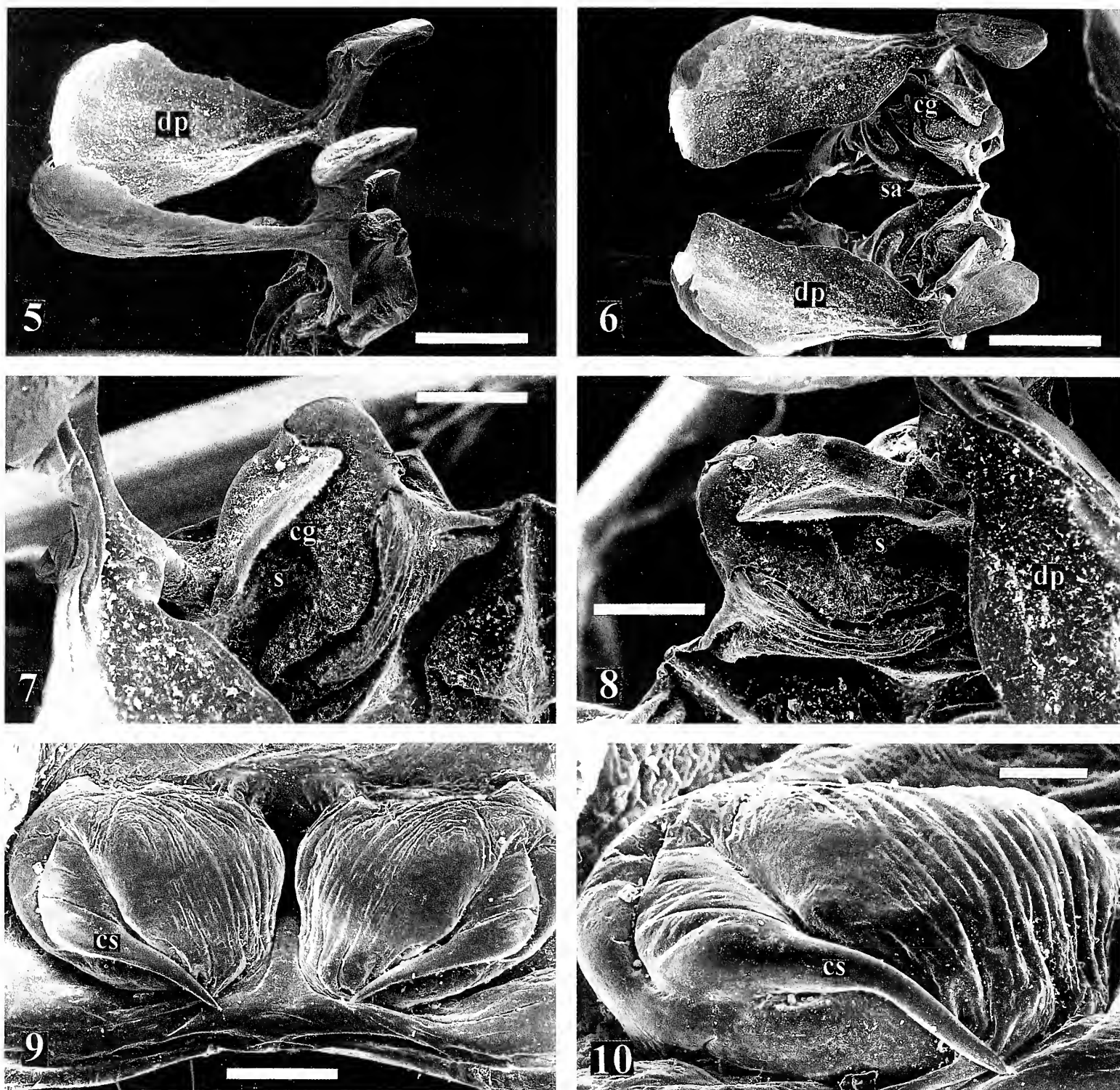
Figure 4.—Schematic lateral view of the position and movements of the female over a spermatophore during the sperm transfer stage. *: location of the gonopods in the internal face of genital operculum. The male continues performing VIB. Other abbreviations: FAP = female approaching; SUP = sperm package uptaking. Parts of spermatophore: 1 = foot, 2 = basal region of stalk, 3 = medial-distal region of stalk which withstands pressure from the females body, 4 = large region of the horn, 5 = distal region of the horn, 6 = copulatory grooves.

Sexual behavior in injured males.—Males of *P. gervaisii* were able to mate even if one of their antenniform legs was injured. The three males captured in this condition (prosoma length: 8.04 ± 0.72 mm) were able to mate normally with non-injured females (prosoma length: 7.46 ± 0.26 mm). One of those males also lacked the tarsus of the third pair of legs (Fig. 1). In addition, one of them mated again and deposited a new spermatophore after a week. In an injured male, the typical light touches of “tapping” became more similar to “vibration”. Such a male always touched the females antenniform legs with only his non-injured leg. When an antenniform leg was partially amputated, its healthy part moved simultaneously with the other leg during the deposition of the spermatophore, vibration and shaking. A female captured in similar condition did not approach the spermatophore.

Pre-insemination spermatophore and female genitalia.—The basal region of the stalk of the intact, pre-insemination spermatophore is inclined at approximately 30° in relation to the soil (Fig. 4). The two parts of the medial region of the stalk are slightly separated from each other. The medial-distal region forms an angle of $50\text{--}55^\circ$ with the basal region. The distal region is wrinkled and has one “copu-

latory groove” in each of the two sides (Fig. 6). These grooves contain in their basal-medial parts the two small sperm packages (Figs. 7–8). The apical part of the spermatophore head has two well developed dorsal horn-like appendages (see Figs. 5–6). The wider region of these horns has irregular edges, unlike the drawing by Weygoldt (1977) in which they appear very uniform. Further, the distal region of each horn is like a “finger” with its dorsal part slightly flattened, but not oriented toward the internal side of the spermatophore as in Weygoldt’s figures. Inside the horns and the distal part of the stalk is a whitish substance that contains abundant spherical cells with many granular bodies. The quantity of the whitish substance is variable among different spermatophores. As with other phrynids, in *P. gervaisii* each of the females gonopods is equipped with a distal, claw-like, hard and dark sclerite (Figs. 9–10). At the base of each is a seminal receptacle (for other details see Weygoldt, 1990, 1998). In this study it has been verified that the female could move the gonopods in all directions, mainly towards both sides. These movements are possible because the females are able to selectively inflate parts of the soft bases of their gonopods, probably by contracting the adductor muscles.

Sperm transfer mechanism.—During



Figures 5–10.—Scanning electron micrographs of spermatophore (5–8) and female genitalia (9–10) of *P. gervaisii*. 5. Lateral view of the spermatophore head. 6. Dorsal view of spermatophore head; showing the well developed dorsal appendages resembling horns. 7. Dorsal-anterior view of the left copulatory groove. 8. View of the right copulatory groove. 9. Internal view of the posterior end of the genital operculum, showing the gonopods with their soft bases and distal claw-like sclerites. 10. Posterior-lateral view of the left gonopod, showing the slight curvature presented in the medial part of claw-like sclerite. Abbreviations: cg = copulatory groove, cs = claw-like sclerite of gonopod, dp = horns of spermatophore, s = place of the sperm package, sa = spine-like apophysis of spermatophore. Scale bars: Figs. 5, 6 = 0.75 mm; 7–9 = 0.25 mm; Fig. 10 = 100 μ m.

sperm transfer, the female moved the genital operculum slightly forwards (Fig. 4) so the two finger-like regions of the spermatophore's horns entered her genital atrium. Meanwhile the ventral side of the opisthosoma, just behind the operculum, rested on the large expansions of the horns. Then the female moved her body up and down slightly and rhythmically (Fig. 4), inserting a claw-like sclerite in

each copulatory groove of the spermatophore. Wrinkles appeared in the medial-distal region of the stalk as the stalk buckled under the pressure of the females body during the copulatory movements. When the female's body was completely over the spermatophore, the spine-like apophysis of the spermatophore (Fig. 6) touched the ventral side of her opisthosoma. Each claw-like sclerite pulled one

sperm package into the apical part of the copulatory groove. Finally, she lifted her body and the sperm packages remained under her claw-like sclerites in the genital atrium. In one case a sperm package, containing both encapsulated and dried spermatozoa, remained attached under the claw-like sclerites for one week. The gonopods of one captured female contained completely dried sperm packages.

Post-insemination spermatophore.—Differences between pre-insemination and post-insemination spermatophores are small but well defined. For instance, the wide regions of the horns of the post-insemination spermatophore are partially oriented downwards (i.e., they are not horizontal in relation to the surface) because of the pressure exerted by the female during her movements over the spermatophore. The finger-like region of each horn is more flattened and the stalk is also more inclined toward the surface. In addition, the apical part of the stalk usually became more folded on itself when the females movements were very intense.

DISCUSSION

Sexual behavior.—Although some of the differences reported here with respect to Weygoldt's work are only due to the fact that the previous descriptions were more general, a number of the observations in the current study are truly novel, such as "pedipalp rubbing" and "female operculum rubbing" and could indicate the existence of geographical variation between the two populations. Further analysis in different populations of other whip spider species may elucidate the degree of geographical variability in the sexual behavior of this group.

The courtship is usually begun by the male in arachnids (e.g., spiders: Foelix 1996; scorpions: Polis & Sissom 1990), although the female can perform some mechanical signals to attract a vagrant male (Polis & Farley 1979). However, like other whip spiders, females of *P. gervaisii* began the courtship (e.g., in a sequence she approached the male and tapped to him as if alerting him to her presence). Probably, the "female initiative" is more favored in whip spiders because of the lack of strong intersexual aggressiveness which is very common in other groups such as camel spiders and scorpions (Punzo 1998; Peretti & Acosta 1999; Peretti et al. 1999). This last

characteristic differs, at least in the studied population, from interspecific aggression. Only individuals of *Phrynus gervaisii* inhabited the nests of the ant *Paraponera clavata* whereas in a near fallen trunk a male of *Paraphrynus laevifrons* (Pocock) was captured (Peretti pers. obs.). A female of *P. gervaisii* killed and ate that *P. laevifrons* male after they were placed together in a terrarium. Agonistic behavior among *P. gervaisii* females included strong touches with their pedipalps and chelicerae.

The various parts of courtship probably serve specific functions. For example, the initial stage may be used to assess sexual receptivity. During this stage, "tapping" and "grasping with unfolded palps" could signal each individual's inclination to continue the courtship. And the male may use additional behaviors to elicit female cooperation. For example, "female operculum rubbing" may have a stimulatory function since the female always became more receptive after the male performed it. Because this behavior has not been observed in other amblypygid species, comparison cannot be made for the Order. However, comparing this behavior with those of other arachnids, such as scorpions, "female operculum rubbing" resembles "tickling" of some buthids (Polis & Sissom 1990). Indeed, males of *Zabius fuscus* (Thorell) often perform "tickling" with the first pair of legs on the females genital operculum. In relation to other behaviors of *P. gervaisii*, further studies are needed to determine whether the audible sound emitted during "pedipalp rubbing" can be detected by the female (directly or via the substratum).

When the courtships of phrynid Amblypygi are compared, all contain "vibrations" or the equivalent (e.g., with more or less shaking movements). This similarity demonstrates the uniformity existing in the courtship of the whip spiders (Weygoldt 1990, 1998, etc.). Like in other arachnids (Eberhard 1994; Peretti 1997, pers. obs.) the copulatory courtship of *P. gervaisii* could function to stop the female from leaving before picking up the sperm packages. However, the ultimate function of the copulatory courtship in a context of cryptic female choice (Eberhard 1991, 1996) has not yet been studied.

It was surprising that the males that had only one antenniform leg were still able to

perform pre- and post-copulatory courtship. Healthy females even cooperated with them (e.g., by moving an antenniform leg close to the males broken one). Weygoldt & Hoffmann (1995) has photographs (figs. 5–10) that show an injured male of *Phrynichus* cf. *ceylonicus* (C.L. Koch 1843) (Phrynichidae) mating with a healthy female. The same has been observed in another phrynichid, *Damon gracilis* Weygoldt 1997 (Weygoldt 1998: figs. 9–13). It would be very interesting to study experimentally the courtship of these accidentally asymmetrical males. The position that a *P. gervaisii* male occupies on the tree bark (always below the female during sperm transfer) agrees with that observed by Weygoldt & Hoffmann (1995) in *Damon diadema* (Simon 1876) (Damonidae). That position could facilitate a better penetration of the claw-like sclerites in the copulatory grooves. In fact, the opened parts of the latter stay facing upwards so that the claw-like sclerites can pull out the sperm packages without losing them.

Sperm transfer mechanism and genitalia.—Copulatory grooves of the spermatophore could act as conductors leading the claw-like sclerites of the females gonopore towards the sperm packages. The two horn-like dorsal appendages of the spermatophore could have a double function: their finger-like anterior region fits tightly in the female genital atrium; meanwhile their wide posterior region offers an effective base in which the female can rest to coordinate her movements. In addition, the distal part of the stalk provides a suspension area when the female rests on the horns. The whitish substance observed inside the horns and part of the stalk could help in the copulatory process by absorbing the pressure exerted by the females body. The spine-like apophysis of the spermatophore might function as a communicatory device since it contacts the ventral face of the female just as her gonopods reach the sperm packages. It would be interesting to determine whether the size of the spermatophore including the copulatory grooves varies among the males, since the size of the claw-like sclerites varies among females from different post-adult stages. In a scorpion, *Bothriurus bonariensis* (C.L. Koch 1842) the spermatophore tends towards an average size that allows all females -independent of their body sizes- to use them without difficulty (Peretti et al. 2001).

The female genitalia of *P. gervaisii* as well as those of other Phrynidae show mechanical properties (e.g., genital appendages that can pick up the sperm packages) which may permit female control of immediate post-copulatory processes by exercising some type of “cryptic female choice” (Thornhill 1983; Eberhard 1996). For example, the sperm packages can be transferred immediately from the gonopods to the seminal receptacles or they can be stored in place which results in dehydration. Although the movements of the gonopods are limited, they would be enough to manipulate and squeeze the sperm packages in order to facilitate the expulsion of the semen (Weygoldt 1977). In addition, the movement of the adductor muscles could induce the movement of the spermatozoa towards the seminal receptacles (Weygoldt 1990, 1999). Weygoldt (1999) mentioned that clear interspecific differences in spermatophores exist among the Phrynidae. The “species mate recognition system” hypothesis (Paterson 1985) is hardly acceptable to explain spermatophore diversity since different types of sexual signals (e.g., tapping, shaking, vibrations, etc.) are typically produced by both sexes during courtship. Although the sculpting of the spermatophore creates a large, hard and elastic head with a minimum of material (Weygoldt 1999), the need for structural integrity does not explain the great diversity in shapes since structural integrity could also be achieved by a more or less uniform morphology. Might the differently sculpted structures have evolved to aid the female in detecting the different parts of the spermatophore and finding the sperm packages? From a sexual selection perspective, the “internal courtship” hypothesis clearly predicts a conspicuous interspecific diversity in male genitalia and a relative uniformity in the females (Eberhard 1985, 1990, 1996). However, future studies are necessary to support this idea for whip spiders since their spermatophores do not seem to have structures to stimulate females. The other sexual selection hypothesis, “the mechanical fit” (Eberhard 1985; Huber 1993, 1995), might not be directly applied to amblypygids because of the apparent lack of close morphological correlation between the male and females genitalia. An evaluation of this hypothesis requires an analysis of all intraspecific differences since, at least in the studied

population of *P. gervaisii*, slight differences were detected among spermatophores of different males (e.g., in the horn-like distal extensions and in the copulatory grooves). Perhaps these differences affect the uptake of the sperm package by the female just as variations in lamella structures of scorpion spermatophores affect sperm transfer (Peretti 1993, 2000; Peretti et al. 2001).

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ORIENTATION AND MOVEMENT OF WOLF SPIDERS *PARDOSA LAPIDICINA* (ARANEAE, LYCOSIDAE) IN THE INTERTIDAL ZONE

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ABSTRACT. Wolf spiders, *Pardosa lapidicina* Emerton 1885, occupy cobble beaches along the tide line about Narragansett Bay, Rhode Island, USA, and move back and forth on the beaches with the tides. I compared the orientation and movement in the low intertidal of three groups with normal access to the entire intertidal zone and a group from the high intertidal prevented from using the low intertidal by a barrier of dense salt-marsh cordgrass *Spartina alterniflora*. They included a group captured in the high intertidal (High), one captured in the low intertidal (Low), one from the low intertidal but not captured (Observed), and one captured behind cordgrass (Cordgrass). The High group moved farther and more unidirectionally than the others, and the Cordgrass group exhibited the most variable orientation of the manipulated spiders. All groups exhibited a roughly southwesterly orientation from the release site. The Low and Observed groups moved shorter distances than the others, and High individuals appeared more strongly inclined to leave the low intertidal than individuals initially positioned there (Low, Observed). Thus, experience likely played a role in the orientation and movement of the spiders.

Keywords: Circular statistics, cobble beach, experience, migration

Highly mobile animals exercise the option of moving about in their habitat to exploit scattered or periodically available resources. This mobility may provide special opportunities that give them an advantage over more sedentary forms. Wolf spiders, *Pardosa lapidicina* Emerton 1885, (Lycosidae) in the vicinity of Narragansett Bay, RI, exhibit the unusual, and possibly novel, habit of moving up and down the intertidal zone with the tides to forage in the intertidal (Morse 1997). Their behavior is thus a mirror image of the much better known aquatic species (fish, crabs, etc.) that move up into the intertidal to forage as the water level rises (Palmer 1995). Perhaps *P. lapidicina*'s closest parallel occurs in some high intertidal amphipods (Talitridae), which orient in response to several cues (e.g., Pardi and Papi 1952; Ugolini et al. 1986; Borgioli et al. 1999).

Given the potentially unique nature of *P. lapidicina*'s movements, it is of interest to inquire what factors govern them and their relationship to behavioral patterns found among spiders and other arthropods. Earlier I demonstrated that *P. lapidicina* hunting in the low intertidal capture significantly more prey than do those in the supratidal area (Morse 1997).

However, this difference does not account for how individuals perform their periodic migratory behavior. In this study I commence to address this question. Members of this population may provide useful insights into this question because they can be divided into subgroups that exhibit different movement patterns. On any given day, some individuals migrate down open cobble beaches to the low-tide line and others remain above the high-tide line at the same time. Censuses with marked individuals have demonstrated that some members of the latter group move down into the intertidal on subsequent days, although it remains unclear whether each one of them will do so at one time or another (Morse 1997). Other members of the population occupy adjacent stretches of the upper part of the cobble beach behind stands of salt-marsh cordgrass *Spartina alterniflora* that blanket a substantial part of the mid-zone region of cobble beaches in Narragansett Bay and prevent the spiders from moving down into the low intertidal. These cordgrass-confined individuals thus do not venture into the low intertidal during the summer and autumn of their first year, though they move over cordgrass stubble in the spring before the plants grow back to block their way (Morse 1997).

Releasing members of these different subgroups of spiders into the low intertidal during the early autumn should provide insight into how they develop and retain their ability to move up and down the tide line. Comparison of those captured in the low and high intertidal should permit separation of any motivational factors to commence movement, and comparison of these two with those isolated behind cordgrass permit evaluation of the role of experience in their performance. The individuals behind cordgrass are born in early summer and hence have had no opportunity to move to the low intertidal. Since one can compare all of these test individuals with undisturbed spiders in the low intertidal, it is further possible to control for any effects of handling.

Orientation is known in spiders, including lycosids (Papi 1955), though in a somewhat different context. Papi (1955) demonstrated that *Arctosa perita* (Latreille 1799), a widespread European species, could select the accustomed side of a stream when displaced, but only if the sky was not heavily overcast. When placed on the water away from the shore, individuals would seek the side from which they had been removed if the sky was clear; if heavily overcast, they would always seek the nearest banking. These spiders used a combination of sun-arc compass bearings, polarized light and local landmarks in orientation. Subsequently, Papi and others (e.g., Papi 1955; Tongiorgi 1959; Leech 1966) demonstrated that *A. perita* shared this trait with several other lycosids, and it has subsequently been discovered in additional spider families as well (Görner 1964). The results presented in this paper address the likely role of experience on a species that probably possesses these basic orientation capabilities common to many other lycosids and other spiders. This paper thus tests the hypotheses 1. that *P. lapidicina* exhibit orientation behavior in their migratory movements that is appropriate to the sites they occupy and 2. that experience enhances their performance at this task.

METHODS

Study animals.—*Pardosa lapidicina* is a small, darkly colored wolf spider of 6–9 mm length, with females somewhat larger than males. Over most of its range in eastern and central North America *P. lapidicina* occupies

rocky streambeds (Kaston 1948; Eason 1969). Its much more poorly known exploitation of intertidal and supratidal areas appears confined to cobble shores, the species thus far not being reported from ledges and sandy or muddy marine shorelines. This high degree of habitat specificity thereby generally limits its marine range to glaciated areas of the northeast, from Connecticut northward. In much of coastal Maine the appropriate cobbles currently lie below sea level, the consequence of a sinking coastline; however, small, dark *Pardosa* C. L. Koch 1848 occupy intertidal cobbles from Mt. Desert Is. (Hancock County) eastward (K. Fink, pers. comm.; S. Zimsen, pers. comm.).

Voucher specimens of *P. lapidicina* have been deposited in the National Museum of Natural History, Smithsonian Institution.

Study area.—I conducted this work at the Haffenreffer Estate of Brown University, Bristol, Bristol County, Rhode Island from August 1994–September 1999. The study area is a cobble beach of 40 m length located on the west shore of Mount Hope Bay, a partially sheltered eastern arm of Narragansett Bay. Tides average 1.4 m, and the mean width of the beach at low tide is 23 m. Most cobbles range from 10–30 cm in the experimental area, with some smooth smaller stones (3–8 cm in length) overlying them at the upper edge of the beach. Some bladder wrack seaweed *Fucus vesiculosus* and a variety of encrusting organisms grow on the larger cobbles.

The study area is bounded on both sides by similar beach that has been overgrown by cordgrass, which covers the middle ranges of the beach (10 m from the top of the beach to 5 m above the low-tide line). The grass is dense, with about 1400 stems/m² (Morse 1997), which prevents *P. lapidicina* behind it from gaining access to the low-tide area. The beach is bounded on its upper side by second-growth forest. The study area is described in further detail by Morse (1997), Bertness (1999:239–242), and Fig. 1.

Experiments.—I investigated the orientation of *P. lapidicina* with four groups of individuals, all tested during low tide in the lower intertidal zone, and referred to throughout as the High, Low, Observed, and Cordgrass groups. Sample sizes in all analyses are 30, 24, 40, and 22, respectively. Members of the

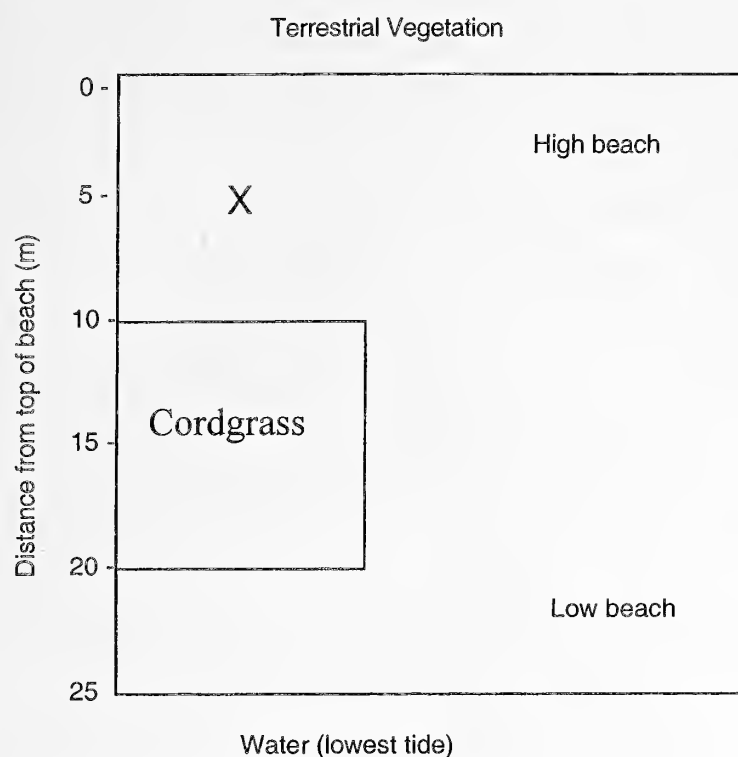


Figure 1.—Diagram of part of study site with both open beach and cordgrass *Spartina alterniflora* areas, as well as capture and release sites of spiders. Capture site of high intertidal group (High) in high-beach area; capture site of low intertidal group (Low) in low-beach area; capture site of group isolated behind cordgrass (Cordgrass) in area denoted by large X; site at which low intertidal, unhandled group observed (Observed) was also in low-beach area. All runs were made in low-beach area, to right of cordgrass in figure.

High group were collected above the high tide line within 5 m of the edge of the forest. They thus had not moved down the beach with the last tide, thereby separating them from individuals in the Low group. Members of the Low group did follow the last tide down into the low intertidal, where they were collected. Another group, the Observed group, also consisted of individuals that moved down the tide line into the low intertidal, where the performances of all the groups were studied. However, they were not collected or manipulated in any way. Lastly, the Cordgrass group was captured immediately above the cordgrass stand, which blocks access of these individuals from the low intertidal, both to the north and south of the beach.

Members of the High, Low, and Cordgrass groups were captured in large plastic containers ($30 \times 18 \times 10$ cm) placed on their side and partially sunken into the cobble so that the spiders could readily be driven into them. The spiders were then transferred to 7 dram plastic vials (5 cm tall, 3 cm diameter). All

individuals of the High and Cordgrass groups were captured within 20–40 m of the test site. I carried members of the four groups about the beach in their vials for periods and distances similar to those of the High and Cordgrass groups. Thus, I handled all three experimental groups as similarly as possible. They were then inverted on a flat stone 1–2 m from the water's edge. Care was taken not to release more than one individual at the same site on a given day, in order to eliminate the possibility that they might follow a line laid down by an earlier tested individual. The vials were left inverted for 2 min, to allow the spiders to acclimate, and then removed. The spiders were subsequently followed for 10 min, and the number, distance and orientation of their movements, as well as their overall displacement from the release site, recorded. We randomly shifted our observation site, as well as hand position in removing the inverted vial, between the north and south side of the release site in order to avoid the chance of systematically influencing the spiders' mean directional movement. Members of the Observed group were located in the low intertidal, and data on them gathered similarly to the other groups. Runs of these individuals commenced after they had come to a full stop.

For purposes of analysis, these data were broken into three observation periods (initial movement, < 2 min, 2–10 min), as well as analyzed as a whole (referred to as mean). Distances were measured with a meter stick, and directions estimated with aid of a clipboard sheet bearing compass orientations that could be quickly calibrated with the beach-forest interface, which lay immediately west of the shoreline. A move consisted of a continuous or nearly continuous directional motion, with instances in which individuals paused in the midst of a bout for no more than 1–2 sec treated as a single move. Moves, as thus defined, generally were interspersed by 15 sec to 2 min. Care was taken to remain 2 m or more from the spiders during this time, in order not to bias their activity. All tests were run under clear skies.

Circular statistics were employed to compare the direction of movements by the spiders. Details of the tests used, and their rationale, can be found in Batschelet (1981) and Zar (1999).

RESULTS

Orientation.—None of the groups (High, Low, Observed, Cordgrass) moved in random directions in any of the observation periods (initial, < 2 min, 2–10 min: Fig. 1; mean). Each measure of all four groups was highly significantly different from a von Mises distribution (circular equivalent to random distribution) at all four observation periods [total = 16 analyses; $Z = 10.21$ – 24.02 ; $N = 20$ – 40 , $P < 0.001$ in all instances: Rayleigh Z Test for circular uniformity (Zar 1999)]. Differences from random would be predicted for all but the initial movements, since the release sites of the experiments lay no more than 1–2 m from the water's edge, and most individuals moved considerably more than a total of 1–2 m in their collective runs. However, initial movements should not be subject to that constraint, since they usually did not approach 1–2 m in length, and they were commenced at the latter distance from the edge.

A natural prediction is that the spiders leaving the site would move directly up the beach; that is, due west (270°), perpendicular to the beach (Papi 1955). However, all of the groups differed significantly from 270° at each observation period [modified Rayleigh V Test for mean direction: Zar 1999 ($\mu = 4.18$ – 6.49 ; $N = 20$ – 40 , $P < 0.001$ in all instances)], in most instances exhibiting a roughly southwesterly direction. Nevertheless, their orientation during the 2–10 min period fell nearer to due west than at other periods (Fig. 2).

Initial moves of the High group differed in direction from those of the other three groups [Table 1: Watson U^2 tests (Zar 1999), with sequential Bonferroni corrections (Rice 1989)]; however, none of the other groups differed significantly among themselves at this stage (same tests). The High group differed from the others in making very few initial moves in a northerly direction, while the others' moves spread more broadly into that direction (Fig. 2). During the first 2 min, only the Observed group differed significantly from the others, largely as a result of retaining an extremely wide directionality of moves, while the other groups conspicuously narrowed their directionality, in that way resembling more closely the performance of the High group in their initial moves. Subsequently, the High group again diverged significantly from the others,

being more strongly directional than the others over the remainder of the observation period. The mean results closely followed those of the 2–10 min group.

Distance moved.—The four groups differed significantly in distance traveled from the original starting point (Fig. 3) ($H = 32.21$, $df = 3$, $N = 116$, $P < 0.001$, Kruskal-Wallis 1-way ANOVA), with most of the difference resulting from the High group moving considerably farther from the starting point than any of the other three groups. Analyzing only the first 2 min in an effort to determine whether initial responses differed among the groups (a possible handling effect) results generally resembled those for the entire 10-min period ($H = 25.76$, $P < 0.001$, same test), with the High group again moving considerably farther than the other groups, and the Cordgrass group moving farther than the Observed group. Data for min 2–10 closely followed those for both the entire 10-min period and the first two min ($H = 21.73$, $P < 0.001$, same test).

The measures reported thus far present total distance from the starting site and do not consider any extra distance resulting from backtracking or otherwise deviating from the eventual direction. Total distances, thus measured, also differed strikingly from random ($H = 43.12$, $P < 0.0001$, same test), generally resembling those of distance from the starting site (Fig. 3). However, the proportional differences between total distance moved and distance from starting point to ending point of a run, a measure of consistency of direction, varied significantly among the groups ($H = 7.82$, $P < 0.01$, same test). In particular, the Cordgrass group moved in much more variable directions than the other three groups (Fig. 4). Thus, though the High group did not move significantly more than the Cordgrass group, it moved significantly farther from the release site as a result of its much more consistent orientation.

Modest differences occurred in the number of moves made by the different groups (Fig. 5) ($H = 9.78$, $P < 0.02$, same test), with the High group somewhat greater than the other groups. Therefore, differences in total movement were primarily a consequence of the length, not frequency, of moves, although numbers of moves contributed somewhat to that disparity.

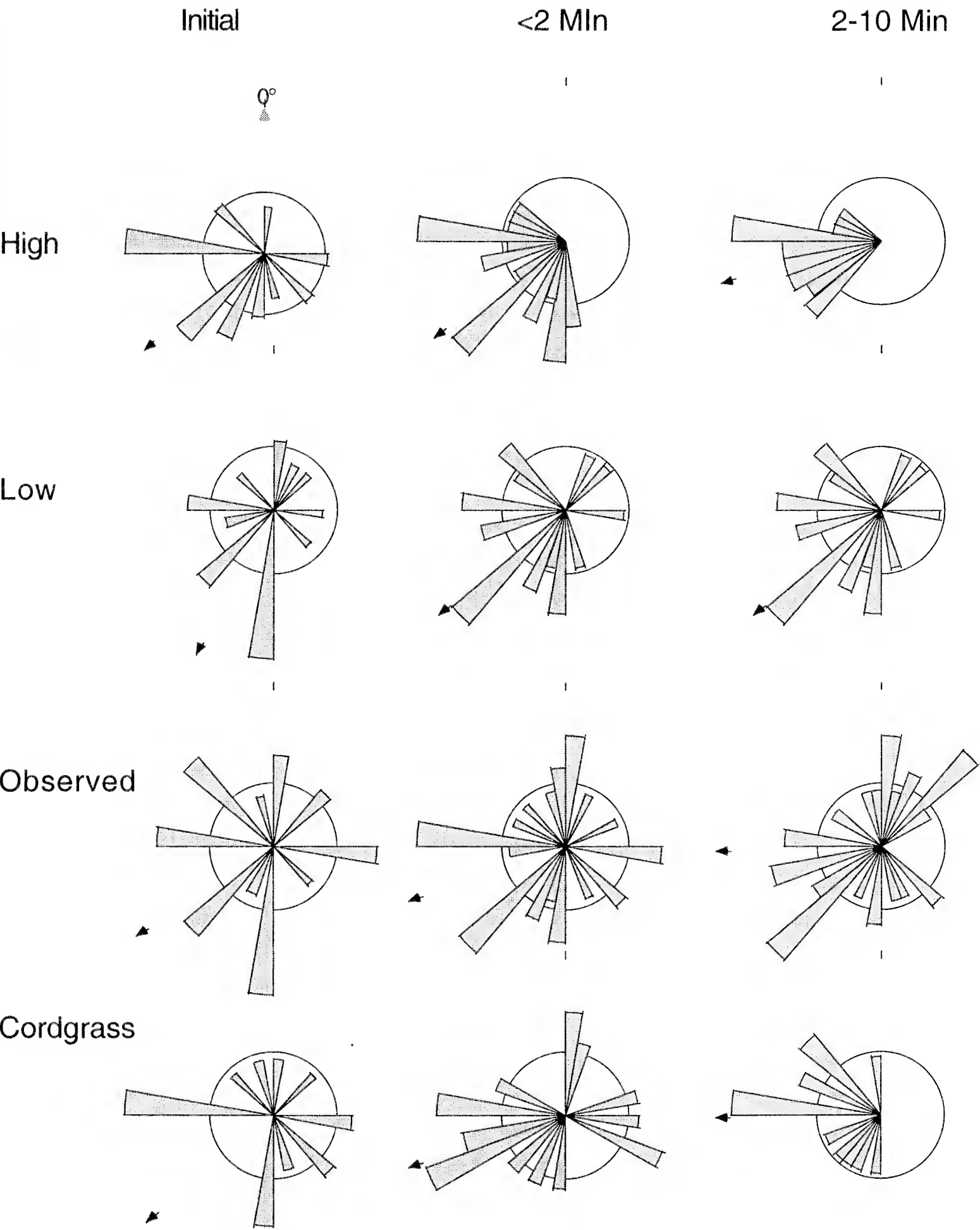


Figure 2.—Rose diagrams denoting directionality of movement during different parts of experimental runs by *Pardosa lapidicina* from the four sites. Mean over entire test period very similar to that of 2–10 min period and therefore not figured. Each wedge in a figure = 10°. Distance from center to periphery of circle = ca. 1.5 observations. Gray arrowhead in upper left figure points to 0° orientation (north). 0° orientation in other figures denoted by thin dash in same position. Black arrow = mean direction of movement of the 20–40 individuals at each stage. Due left = 270° (west), a trajectory taking spiders directly up the beach. Rose diagrams are circular histograms with wedges scaled to represent the relative proportions of measurements falling in each class interval (Zippi 1987–2000).

Table 1.—Differences in orientation among the four groups of spiders at different periods of their trials, presented as U^2 and significance levels. * = $P < 0.05$ in Watson U^2 tests (Zar 1999) with sequential Bonferroni corrections (Rice 1989), U^2 with no *: $P > 0.05$.

PERIOD	GROUP		
Initial	Low	Observed	Cordgrass
High	.258*	.261*	.296*
Low		.177	.212
Observed			.135
<2 min			
High	.079	.223	.125
Low		.110	.128
Observed			.265*
2–10 min			
High	.547*	.837*	.366*
Low		.197	.097
Observed			.315*
Mean			
High	.381*	.643*	.141
Low		.304*	.089
Observed			.274*

DISCUSSION

Differences among groups.—Members of the different groups varied in several important ways. First, members of the High group differed markedly from the others in both their focused orientation and the maximum distance they moved away from the release site. They

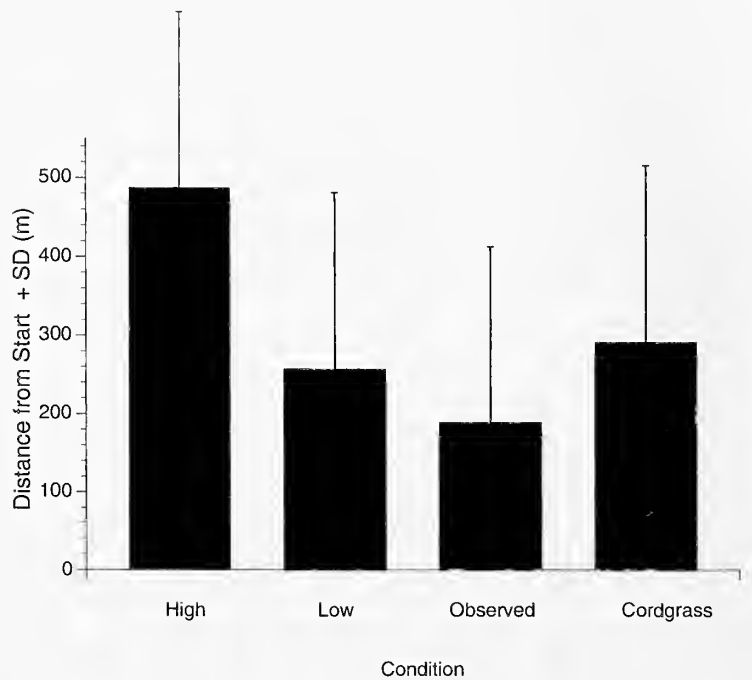


Figure 3.—Distance ($\bar{x} \pm \text{SD}$) moved by four groups of spiders ($\pm \text{S.D.}$) over 10 min period following release.

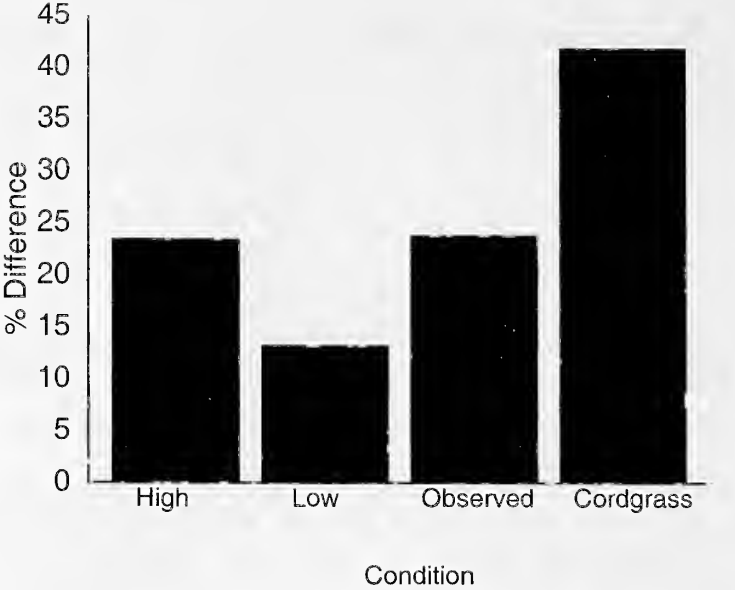


Figure 4.—Percent difference between total distance moved and distance from start by four groups of spiders over the 10 min period following release.

thus responded as if they were aware of their location and that it was unsatisfactory to them. This behavior is consistent with them being familiar with the intertidal area, even though they did not occupy it on the days they were tested. The demonstrably naïve Cordgrass individuals exhibited the most variable orientation of any of the three experimental groups (Fig. 4). Though moving so much that their total travel distance did not differ significantly from that of the High group, their straight-line distances differed significantly, because of their constant shift in orientation. Thus, although both groups appeared highly motivated to leave the release site, the High group’s experience apparently permitted them to move away from it more effectively than the Cord-

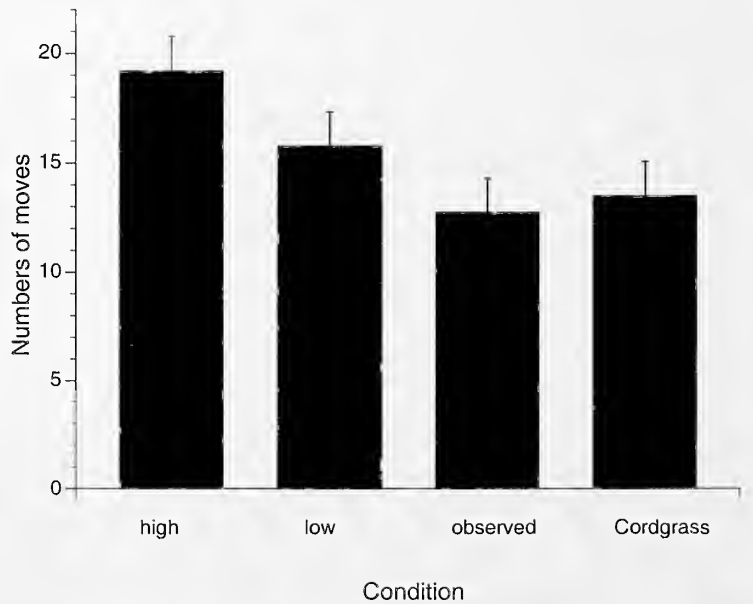


Figure 5.—Number of moves by four groups of spiders ($\pm \text{S.D.}$) over the 10 min period following release.

grass group. If so, then accurate movement up and down the tide line depends on learning from earlier experiences in the habitat, which the Cordgrass individuals lack. The shorter distances moved by the Low and Observed groups may reflect their being at or near sites they had just been occupying. The higher variation of direction by the Observed group may reflect a somewhat different motivational state from that of the other individuals, though their similarity of performance to the Low group reflects their perceived quality of the site. The results thus suggest that experience (and probably learning) plays a role in honing the exploitation patterns of the spiders. Spiders and other small invertebrates are known to be capable of learning responses to simple stimuli such as these (Morse 2000; Heinrich 1979; Vet & Papaj 1991).

Although one might question whether the differences reported between experienced and inexperienced individuals produce enough benefits to generate and maintain such behavior, the increase in proficiency likely translates into extra hunting time. It may also mediate risk encountered from being swept off the site by unanticipated waves (Morse 1997), which cast them into water containing large numbers of small predatory fish, primarily silversides *Menidia menidia* (pers. obs.). These spiders move formidable distances (> 40 m) during a single trip up and down the beach, and the differences in time required to execute these movements should suffice to enhance the value of such a difference. Such abilities are likely obtained during early instars, because the spiderlings begin to move extensively down the tide line by their third instar, in July (Morse 1997). I have no data on their orientation abilities at this time, but Papi and Tongiorgi (1963) reported that young *Arctosa perita*, a European lycosid, develop orientation abilities early in life.

These spiders capture significantly more prey in the low intertidal than they do above the tide line (Morse 1997). Hence, condition could account for the relatively low movement rates of both the Low and Observed groups, which occupied positions from which they might have captured prey immediately before we recorded their activity levels. Hunger affects the activity rates of some (Walker et al. 1999; Persons 1999), though not all (Provencher & Reichert 1991) spiders. If only

hungry spiders moved into the lower intertidal, as seems likely (Morse 1997), it is improbable that movement of the High group would significantly exceed those of the other groups, however. Further, light-bodied cursorial lycosid species [*Pardosa milvina* (Hentz 1844)] appear less likely to modify their activity rates in response to different levels of starvation than did heavy-bodied lycosids [*Hogna helluo* (Walckenaer 1837)] (Walker et al. 1999).

Orientation.—All four groups moved in a predominantly southwesterly to westerly direction over the course of the manipulations. This result could not have been a consequence of their collection sites, because roughly similar numbers of individuals taken for the High sample came from sites to the northwest, west, and southwest of the release area, and similar numbers from the Low samples came from sites to the north and south of the release area. Additionally, I randomly shifted the observation site, so that roughly half of the spiders were observed from the north side and half from the south side. Papi & Syrjämäki (1963) found that *Lycosa fluviatilis* (Blackwall 1861) [= *Pardosa agricola* (Thorell 1856)] from sites normally without access to the unbroken sky performed less consistently in orientation experiments than did individuals from adjacent barren areas that provided unobstructed views of the sky. The markedly greater variance in direction of the Cordgrass group is consistent with this factor as well as an unfamiliarity of the intertidal sites.

The only closely comparable information on orientation by displaced individuals I have found involves *Pardosa pullata* (Clerck 1757), a common species along European shores. *Pardosa pullata* exhibited a well developed pattern of orientation when displaced down the beach (Bristowe 1958). All members of a sample of 50, so displaced, moved up the beach, either immediately or by quickly angling around to an up-the-beach orientation, which they then adopted. Several of the *P. lapidicina* placed low in the intertidal similarly first moved toward the water before angling about and moving up the beach. In some instances the *P. lapidicina* reached the edge of the nearby water 1 m or more seaward of their release site before changing directions and moving up the beach. In his single test, Bristowe (1958) reported none of the variability

in performance that I found in samples of *P. lapidicina* taken from different sites, but his brief report contains so little detail that it is not possible to eliminate the possibility of such variance.

Other lycosids, including members of the genus *Pardosa*, are well known to exhibit orientation abilities (Papi 1955; Tongiorgi 1959; Leech 1966), which depend at least in part on the use of polarized light, in some instances known to be mediated through the anterior medial eyes (Papi 1955; Ortega-Escobar & Muñoz-Cuevas 1999). When placed in a strange environment with a polarized light source these spiders oriented in a direction that would normally return them to their site. For instance, if displaced from a shoreline site, they oriented and moved in the direction that would normally move them back to that shore (Papi 1955). If released under an overcast sky, however, they moved toward the closest object (Papi & Tongiorgi 1963), apparently using conventional visual stimuli under those circumstances. Although I did not test for the precise mechanism involved, the consistent tendency of all groups of *P. lapidicina* to move in a southwesterly direction, despite their differences in precision, is also consistent with these spiders using some form of astronomical cues in orientation.

Dondale & Redner (1990) report that both *P. labradorensis* (Thorell 1875) and *P. groenlandica* (Thorell 1872) frequent intertidal cobble and stony beaches of Atlantic Canada and Greenland. These species are likely candidates to exhibit behavior similar to that of the *P. lapidicina* described in this paper. Curiously, Dondale and Redner do not list intertidal cobble among the habitats frequented by *P. lapidicina*. The literature thus suggests that such behavior is uncommon among spiders in the intertidal area, but the habitat has been so poorly studied from this perspective (Morse 1997) that this conclusion must be regarded as provisional.

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SHORT COMMUNICATION

A NEW OGRE-FACED SPIDER (*DEINOPIS*) FROM THE GAOLIGONG MOUNTAINS, YUNNAN, CHINA (ARANEAE, DEINOPIDAE)

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ABSTRACT. The present paper describes *Deinopis liukuensis* new species, from the Gaoligong Mountains, Yunnan Province, China. This is the first mature deinopid described from China.

Keywords: Araneae, Deinopidae, *Deinopis*, taxonomy, Gaoligong Mountains, Yunnan, China

The spider family Deinopidae was first recorded from China by Wang (1983), who reported a juvenile individual of *Deinopis* sp. from Jinghong, Yunnan Province. The present paper describes the first mature individual, a male, from China. The type specimen is deposited in the College of Life Science of Hunan Normal University. The specimen was collected by the second Sino-American expedition to the Gaoligong Mountains during June and July 2000.

Measurements are in mm. The following abbreviations are used: AER = anterior eye row; AL = abdomen length, ALE = anterior lateral eye, AME = anterior median eye, AME-AME = interval between AMEs, AME-ALE = interval between AME and ALE, AW = abdomen width, CL = carapace length, CH = clypeus height, Con = conductor, Cym = Cymbium, CW = carapace width, Em = embolus, Fem = femur, Metat = metatarsus, MOQ = median ocular quadrangle, MOQA = MOQ anterior, MOQP = MOQ posterior, Pat = Patella, PER = posterior eye row, PLE = posterior lateral eye, PME = posterior median eye, PME-PME = interval between PMEs, PME-PLE = interval between PME and PLE, Tar = tarsus, Tib = tibia, TL = total length.

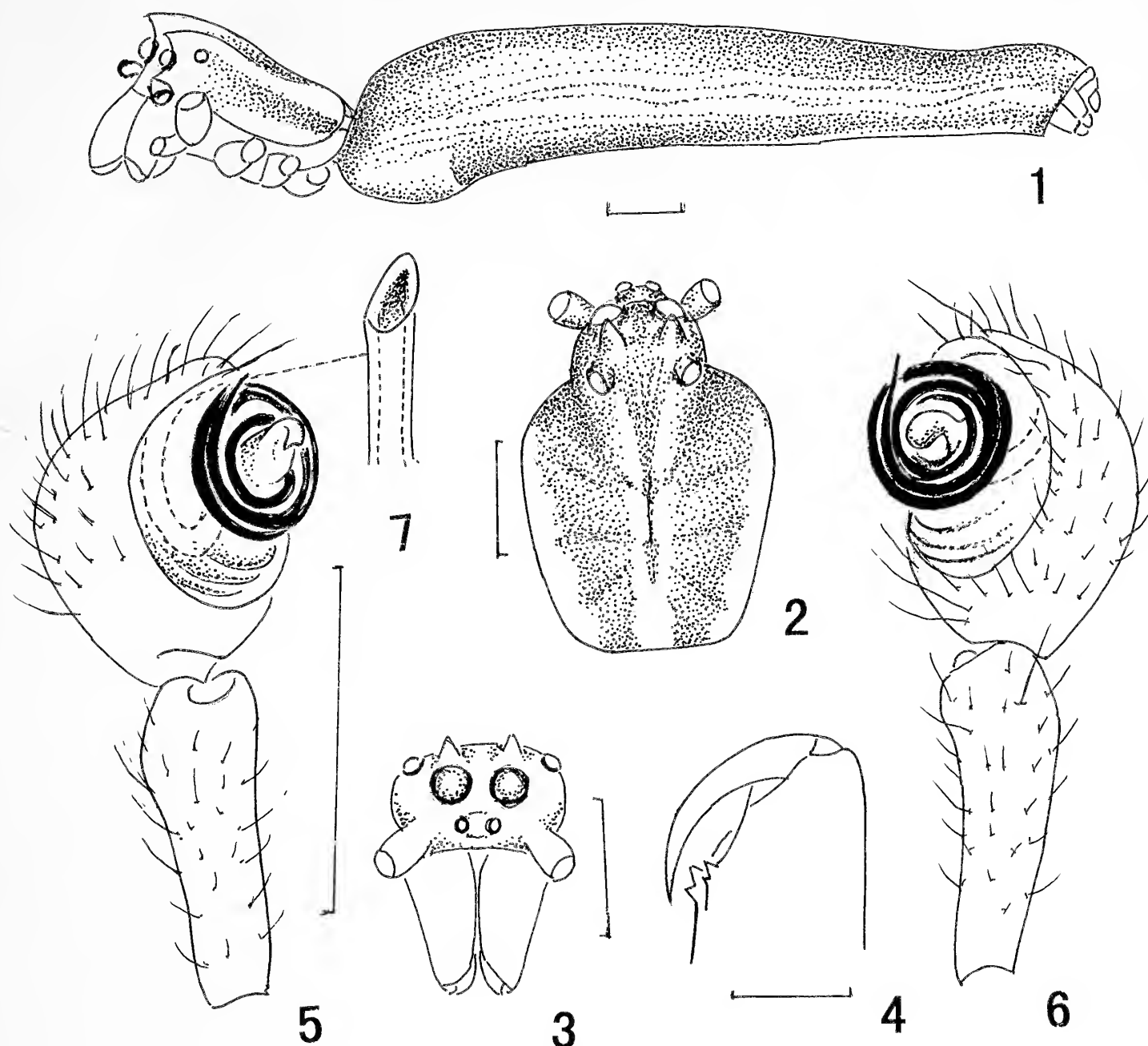
Deinopis liukuensis new species
Figs. 1–7

Material examined.—Holotype male, Mt. Gaoligong, Liuku, Yunnan Province, P. R. China, 25.51337°N, 98.50992°E, elevation 800 m, 26 June

2000, Heng-Mei Yan, deposited in the College of Life Science of Hunan Normal University (Type no. 00-LK-1).

Diagnosis.—Deinopids have been described and illustrated by Chickering (1963), Chrysanthus (1967, figs. 47–51), Coddington (1990), Davies (1988, fig. 7), Kraus (1956), Lehtinen (1967, figs. 33–41), Schenkel (1953, fig. 8), Schiapelli & Gerschman de Pikelin (1957) and Wang (1983, figs. 1–3). We have compared the new species with those described in these references and find it is most similar to *Deinopis diabolica* Kraus 1956 from El Salvador, but can be separated by the following characteristics of *D. liukuensis* (vs. *D. diabolica*): length ratio of carapace: abdomen length 1:3.55 (1:1.76), ratio of AME:PME diameter 1:2.38 (1:4.12), horn-shaped processes on carapace smaller, shorter than that of *D. diabolica*, tip points forward (larger, longer, than that of *D. liukuensis*, tip points to anterolateral side), coiled embolus of left palpal organ, ventral view, ends at 12 o'clock (3 o'clock), and the shape of the embolic terminal transparent sheath cylindroid (Fig. 7) (rhomboid [Kraus, 1956: 169, fig. 5])

Description.—Male: Cephalic region pear-shaped, widest behind, narrower than the trapezoidal thoracic region (Figs. 1, 2), median band and lateral margins yellow grayish brown. Lateral longitudinal bands gray-black. AER strongly procurved; ALE situated on the top of a club-shaped stalk. PER strongly recurved, behind each PME an orange-brown horn-like process that is clothed with



Figures 1–7.—*Deinopis liukuensis* new species. 1. Body, lateral; 2. Carapace, dorsal; 3. Carapace, front; 4. Chelicera; 5. Palpal organ, prolateral; 6. Palpal organ, retrolateral; 7. Embolic terminal transparent sheath. Scale lines = 1.00 mm.

white scale hairs. Sternum elongate, triangular, median portion and lateral margin covered with silver scale hairs. Chelicera yellow-gray, both margins with 2 teeth (Fig. 4). Endite longer than wide, yellow-gray dotted with grayish black spots, its external edge medially concave, kidney-shaped, internal edge ornamented with brown scopulae. Labium as long as wide, white-gray, covered with small scale hairs. Legs slender, coxa and trochanters I and II grayish black, trochanters III and IV dotted with yellow-gray spots; distal segments yellow-gray to yellow-grayish brown. Three claws, the upper claws with 4 teeth. Abdomen clothed with white scale hairs, black short spines and fine hairs; with long band-like folium at the median, on its two sides yellow-gray striae alternating with black ones. Abdomen ventrally grayish black, middle darker than side.

Measurements: holotype male, TL 12.30, CL 2.70, CW 2.40 (widest)–1.00 (narrowest); AL 9.60, AW 1.60. Eye size and intervals: AME 0.16 (small-

est), ALE 0.22, PME 0.38 (largest), PLE 0.24; AME-AME 0.13, AME-ALE 0.47, PME-PME 0.16, PME-PLE 0.38; MOQ L 0.61, MOQA W 0.42, MOQP W 0.89; CH 0.06 < AME diameter, sternum L 1.80, W 1.10, labium L 0.50. Leg formula: 1243. Palp and leg lengths (Femur + Patella + Tibia + Metatarsus + Tarsus = Total): Palp: 2.50 + 0.40 + 1.20 + (absent) + 0.90 = 5.00; Leg I: 10.50 + 1.20 + 10.80 + 15.80 + 4.10 = 42.40; Leg II: 9.50 + 1.30 + 9.10 + 8.20 + 3.30 = 22.40; Leg III: 7.40 + 1.30 + 6.50 + 5.60 + 1.30 = 21.10; Leg IV: 7.50 + 1.30 + 6.60 + 5.70 + 1.10 = 22.20.

Female: Unknown.

Etymology.—The specific name is derived from the type locality.

Distribution.—At present, this species is known only from the type locality in Yunnan, China.

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SHORT COMMUNICATION

FEEDING IN *MAXCHERNES IPORANGAE* (PSEUDOSCORPIONES, CHERNETIDAE) IN CAPTIVITY

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ABSTRACT. The feeding behavior of the cave pseudoscorpion *Maxchernes iporangae* Mahnert & Andrade 1998 was studied in the laboratory. We also investigated aspects such as preference and frequency. Nymphs are more active in prey capture. Cannibalism is uncommon. The frequency of feeding of adults was about once a month, with an increased rate for females during the reproductive period.

Keywords: Pseudoscorpiones, feeding behavior, feeding frequency, Chernetidae, *Maxchernes*

Pseudoscorpions are predators of other arthropods. The organisms consumed by pseudoscorpions kept in captivity included larvae and adults of *Drosophila* sp. (Gilbert 1951; Levi 1953; Goddard 1976), Isoptera (Brach 1978; Hahn & Matthiesen 1993a), Collembola (Wood & Gabbutt 1979a, 1979b; Johnson & Wellington 1980), Psocoptera (Levi 1948, 1953), and larvae and adult of cucujid and tenebrionid beetles (Levi 1948, 1953). Information about pseudoscorpion prey and predators can be found in Jones (1975).

Chthoniidae, Neobisiidae and some related families masticate the prey with their chelicerae; at the same time the food is digested by a fluid from the oral cavity. Later, the digested contents are ingested (Gilbert 1951; Weygoldt 1969). Other groups (e.g., Olpiidae, Garypidae, and all Cheliferoidea) use the chelicerae to make a hole in the body wall of the prey, through which an enzymatic fluid is injected. The digested contents are then ingested (Feio 1942; Gilbert 1951). After digestion, the ingested material that has not been used is transformed into crystals, probably guanine (Gilbert 1952), which is stored in the rectal pocket and excreted from time to time. A comprehensive review of the digestive tract and nutrition of pseudoscorpions is given in Heurtault (1973).

The present study gives further information about feeding in pseudoscorpions, specifically regarding feeding behavior, preference and frequency in the chernetid pseudoscorpion *Maxchernes iporangae* Mahnert & Andrade 1988, a species living in a subterranean habitat.

Individuals of *Maxchernes iporangae*, which are approximately 2 mm in length when adults (see Mahnert & Andrade 1998), were collected on fru-

givorous bat guano piles from Alambari de Baixo Cave (SP-012, 24°33'15" S and 48°39'55" W), situated in the Ribeira River Valley (São Paulo State, Brazil). This species seems to be restricted to this kind of guano in this particular cave (Mahnert & Andrade, 1998; pers. obs.). Collections and observations were made between February 1996 and February 1998.

The pseudoscorpions were placed with guano in small closed containers and transported to the laboratory, where some pseudoscorpions were kept in groups (up to 18 individuals) in transparent plastic boxes (9 cm length x 6 cm width x 2.5 cm height). Others were kept individually in glass Petri dishes (2.5 cm diameter x 1.5 cm height). All containers contained moistened guano or fine sand on the bottom, and were kept under almost constant darkness and at a temperature of 21.0 °C ± 2.0. This temperature is similar to the temperature of the cave inhabited by the species studied. Regarding the use of alternative substrates, we preferred the use of guano. However, this material rots with time and accumulates fungi, needing to be replaced. Because sometimes it was not available at the laboratory, we used fine sand.

In order to analyze the feeding frequency, the pseudoscorpions were fed twice a week. Each isolated adult received one live adult of *Drosophila* sp. (slightly larger than an adult *M. iporangae*). After six hours, the dish was examined. The feeding was considered effective if the pseudoscorpion was found eating the prey. Other items were also offered to adults: psocopterans, tineid moth larvae, psychodid dipterans, collembolans, *Endecous* sp. cricket nymphs (which occur in the same cave as the pseudoscorpions) and isopods (from the same gua-

no piles as the pseudoscorpions). The last two animals were offered to determine if they could be natural prey of *M. iporangae*. The other animals were offered because they were available in the laboratory, although they did not occur in the caves studied. The initial purpose of trying different food items was to maintain the pseudoscorpions in the laboratory, since the cave is located 5 hours from São Paulo, because the original objective of the study was to follow their life cycle. Nymphs were initially offered live *Drosophila* sp. larvae. Later, a dead adult *Drosophila* sp. was left in each Petri dish with nymphs. More than thirty observations on feeding behavior were performed with isolated and/or grouped pseudoscorpions.

Voucher specimens, collected at the same guano deposit where the type specimens were collected, are deposited at the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP).

Feeding behavior.—Adults of *M. iporangae* moved relatively slower than nymphs and mostly attacked prey by quick movements of the pedipalps when the prey was near. The nymphs attacked prey more readily, pursuing prey over relatively longer distances. Protonymphs were more active in prey capture than later instars. This was also observed for *Paratemnoides minor* (Balzan 1892) (Atemnidae) (see Hahn & Matthiesen 1993a) and is probably related to the larger feeding needs of the young, in order to allow faster growth and development.

Maxcheres iporangae grasped the prey with the palpal chelae and immobilized it with their poison. The time taken to paralyze the prey varied. The time in which the pseudoscorpion kept the prey between the palpal chelae also varied, reaching up to 10 min. In some cases, the grasped drosophilid was immobilized in a few seconds, in others, it took longer. Probably the immobilization time is related to the prey region pierced (Feio 1942), and/or to the prey sensitivity and size. After immobilization, the prey was passed to the chelicerae, where it remained for a variable time, sometimes exceeding 2.5 h. On some occasions, the pseudoscorpions were observed piercing a prey in different positions, a behavior also recorded for *Dactylochelifera latreillei* (Leach 1817) (Cheliferae) by Gilbert (1951). This behavior allows more efficient utilization of the prey by feeding at multiple points.

During feeding, the prey was held only by the chelicerae, and the palps were kept free and directed laterally, in a characteristic defensive posture, as observed for other pseudoscorpions (Gilbert 1951; Weygoldt 1969). The palps were used to attack other pseudoscorpions that occasionally approached. Individuals of *M. iporangae* were often observed walking with prey held in their palps or even by the chelicerae, until they found a secure or hidden place, where they stopped and started feeding. This

aspect, frequently observed in grouped pseudoscorpions, was practically absent among isolated pseudoscorpions. This behavior may represent a response to the recognition of other pseudoscorpions in proximity and may avoid prey theft by another pseudoscorpion.

The sharing of prey by up to three pseudoscorpions was observed among pseudoscorpions kept in groups. On these occasions, the pseudoscorpions were sufficiently separated so that they did not touch each other. However, if some disturbance occurred, such as prey movement or the approach of another individual, the pseudoscorpions became agitated, attacking each other, without releasing the prey and pulling on it, until one individual succeeded in moving off with the prey. The partition of prey was earlier recorded for nymphs and adults of *Paratemnoides elongatus* (Banks 1895) (Atemnidae), however, without aggressive interactions or attempts to take the prey (Brach 1978).

Grooming behavior was often observed. The most important grooming organ is the serrula exterior of the movable fingers of the chelicerae (Weygoldt 1969). In *M. iporangae* the palpal fingers were cleaned by drawing them through the chelicerae; the chelicerae were cleaned by rubbing each other; and the palpal coxae by cheliceral rubbing. The grooming occurred just after the prey was placed in the dish with the pseudoscorpion, during and at the end of feeding, after the prey was released. The grooming of the palpal fingers before feeding, when the prey was placed in the dish, would possibly have the function of improving the capacity of recognition and detection of the prey and its location by using the palpal trichobothria. Such behavior is usual in other species of pseudoscorpions (Weygoldt 1969; Heurtault 1973).

Feeding preference.—When live fly larvae (*Drosophila* sp.) were offered as food to protonymphs of *M. iporangae* that hatched in captivity, only two attacks were observed. The protonymphs only pinched the prey by quick movements of the pedipalps, without taking the prey. The same happened with small collembolans, except on one occasion, when a protonymph grasped and passed it to the chelicerae.

Prey rejection probably was the main cause of the low survival rate (4%) observed among protonymphs, which is considered to be the more active metabolic instar in many species of pseudoscorpions that possess a free protonymph phase (Levi 1948, 1953; Goddard 1979; Hahn & Matthiesen 1993a).

Good survival rates (increased from 4% to 40%) were obtained when dead adult flies were placed in the dishes with protonymphs. Although the prey was large and feeding was rarely observed, the mortality rate of these protonymphs decreased, indicating that the nymphs were probably feeding. In

addition to drosophilids, deutonymphs and tritonymphs accepted other food, such as tineid larvae and psocopterans. Adult pseudoscorpions accepted fly larvae in addition to dead or live adult flies, but, in that case, at a lower frequency than the acceptance of adult flies. Many times they only pinched the prey without grasping it, then rejected the food offered. Other prey accepted were psychodid dipterans, psocopterans and tineid larvae, the later in higher frequency than the former. We should stress that psocopterans and tineid moths are common in guano deposits, even in similar frugivorous bat guano (such as in Casa de Pedra cave—see Gnaspini 1989a, b), but not in this guano pile, so far. Collembolans were not taken, which is probably related to the collembolan's agility. The possible natural prey (*Endecous* nymphs and isopods) were not taken at all.

On one occasion, in the field, a pseudoscorpion was observed dragging a prey with its palp. Both were collected and brought to laboratory where the pseudoscorpion was identified as an adult male and the prey as an early nymph of an undetermined species of seed bug (Heteroptera, Lygaeidae). The occurrence of nymphs and adults of two undetermined species of the family Lygaeidae inhabiting guano piles of frugivorous bats in the Alambari de Baixo Cave was recorded by Gnaspini-Netto (1989a, b). These heteropterans were considered by Gnaspini (1992) to be guanobites, a word used to define organisms which, in caves, inhabit guano deposits exclusively, where they complete their life cycle. Because of the preying event directly observed in the field and because of the probable restriction (considering the cave population) of these bugs to the same guano piles where *M. iporangae* is present (Gnaspini & Trajano 2000), it is probable that these bugs are one (and maybe the principal) of the natural prey of this species. Unfortunately, it was not possible to offer these animals to pseudoscorpions in captivity.

There are few studies concerning feeding preference of pseudoscorpions. Weygoldt (1969) reported that chernetids prefer insects, such as small dipterans, psocopterans and beetles, and that many species can be maintained on drosophilids, as we did with the studied species.

Cannibalism.—Weygoldt (1969) considered cannibalism to be a rare event among pseudoscorpions, and that it would occur among animals kept in captivity without food for a long time, especially considering that older or injured animals could be attacked by others. Considering chernetids, Levi (1953) did not observe cannibalism among individuals of *Lamprochernes minor* Hoff 1949 kept in captivity. On the other hand, considering other Cheliferioidea (in which Chernetidae is included), Levi (1948) observed cannibalism among protonymphs of *Chelifer cancroides* (Linnaeus 1758)

(Cheliferidae). Varied results occurred among Atemnidae: *Paratemnoides elongatus* did not show cannibalism (Brach 1978), whereas *P. minor* (Hahn & Matthiesen 1993b) did.

We observed only three cases of cannibalism in *M. iporangae*, all three with alternative food (flies) available. First, a protonymph fed on a second protonymph kept in the same Petri dish. The victim was inside its molting chamber, in a characteristic torpid condition that precedes the molt, thus unable to move or defend itself. On another occasion, an adult female was observed preying on a recently hatched protonymph. Considering that we had 12 breeding females with a total of 118 hatched nymphs, it gives a rate of less than 1% cannibalism. Finally, a female was found feeding on her brood sac, which was previously abandoned outside the nest at an advanced stage of development. Considering that she did not abandon her eggsac to specifically feed upon it (she probably found the eggsac by chance), and that we do not know if females can recognize abandoned brood sacs as their own, we can not even assure that this is a case of intentional cannibalism. The last two cases occurred with adults kept individually (from other adults, but not from their own brood). In general, cannibalism can be considered uncommon in *M. iporangae*, especially considering that (1) it did not occur among adults kept in groups, and (2) it was recorded only three times (ca. 1%) over 310 observations done for *M. iporangae* during this study.

Feeding frequency.—Generally, adult pseudoscorpions of *M. iporangae* ate about once a month. The average number of prey eaten per month was 1.14 ± 0.50 s.d. ($n = 47$). There are few studies on feeding frequency of other pseudoscorpions. For comparison, Levi (1948) reported that adults of *Chelifer cancroides* can feed once or twice a week.

When sexes were analyzed independently, the monthly average feeding frequency of females of *M. iporangae* was 1.27 ± 0.50 ($n = 33$); and of males was 0.83 ± 0.34 ($n = 14$). We observed that 85% of males had a feeding frequency between 0.4–1.19, whereas in 75% of females the frequency was between 0.8–1.99 times a month. Although the confidence interval for feeding frequency of males and females overlap, Mann-Whitney rank sum test ($T = 213.0$, $P = 0.004$) showed that the sexual difference between frequencies is statistically significant. In addition, the monthly average feeding frequency of females after breeding increased to 1.50 ± 0.27 ($n = 11$), but this increase is not significant (overlap of confidence intervals and Mann-Whitney rank sum test— $T = 263.0$, $P = 0.222$). The energy spent for the nutrition of embryos and for the time spent inside nest chambers may be responsible for the increase (although not significant) in feeding frequency of females in the reproductive period. This is also common in other arachnids that

spend some time with their brood without feeding (e.g., laniatorean harvestmen, Gnaspini 1995).

Similarly, an increase in the feeding activity of animals having recently left molting chambers was observed in two cases. The monthly average feeding frequency of a recently molted adult female was 3.7 during the three months subsequent to exiting the molting chamber. The second case is a tritonymph, which increased its feeding frequency to 2.0 also for three months. It is expected that pseudoscorpions increase their feeding frequency after the molt, due to having spent a long time without food. This increase is expected to be larger in early stages because they are more active and feed more frequently (Levi 1948; Hahn & Matthiesen 1993a). The fact that our observations do not agree with this statement is probably due to the extremely low number of cases observed.

An ecological study focusing on this species in the field is presently being conducted by the senior author, including food preferences, and should give additional information that could resolve some unanswered questions.

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SHORT COMMUNICATION

NOTES ON THE NATURAL HISTORY AND HUNTING BEHAVIOR OF AN ANT EATING ZODARIID SPIDER (ARACHNIDA, ARANEAE) IN COLORADO

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ABSTRACT. The ant hunting behavior of *Zodarion rubidum* (Araneae, Zodariidae) is described from specimens collected in Colorado, USA. Like other members of this genus, *Z. rubidum* constructs igloo-shaped stone retreats under rocks and feeds on ants. Details of the prey capture behavior are provided including initial and subsequent reactions of ants to the bites of *Z. rubidum* and data on the time it takes for ants to become completely paralyzed as a result of the bites.

Keywords: *Zodarion*, myrmecophagy, spider-ant association, femoral organ

Zodarion rubidum Simon 1914 is the only species of this genus of Zodariidae reported from North America (Vogel 1968; Jocqué 1991; Bosmans 1994, 1997). It had previously been reported from Pennsylvania (Vogel 1968; Bosmans 1994, 1997). Participants of the Colorado Spider Survey, Nina Shilodon and Steven Bonham, discovered the first population of this small spider in Colorado. The Colorado population lives under rocks inside igloo-shaped stone retreats in a variety of habitats including xeric and riparian areas. Most members of the genus build these retreats (Simon 1914; Harkness 1977; Jocqué 1991; Bosmans 1994; Pekár & Král 2001). The spider forms the retreat by overlapping small pieces of debris (soil particles, rocks, and plant material) on a silken framework using its palps and front legs to manipulate material (see figure 3 in Pekár & Král 2001). Although Vogel (1968) did not find these retreats in a population of *Z. rubidum* found in a rock quarry in Pennsylvania, it is likely that they are present in that population as well. It is unknown whether this species extends across the US between Pennsylvania and Colorado. Although it has not previously been reported from collections from those areas, collectors not specifically searching for them may easily overlook the small retreats.

Spiders in the genus *Zodarion* are compulsory ant eaters, or myrmecophages (Simon 1874, 1914; Santschi 1908; Schneider 1971; Harkness 1976, 1977; Jocqué 1986, 1991; Couvreur 1990a). The purpose of our study was to examine the ant hunting, or myrmecophagic, behavior of these spiders in more detail in a controlled laboratory setting.

Thirty immature spiders were collected in July 1999 from a riparian area off W. 56th Avenue west of the town of Golden, Colorado in Jefferson County (39°48' N, 105°14' W; 1,859 m). Spiderlings were individually housed in Petri dishes measuring 55 or 90 mm in diameter. Loose soil and wet cotton were provided for each spider. A fluorescent light was placed on a timer providing a 12:12 light:dark cycle. This proved to be an important element of our protocol because these spiders appear to be strictly nocturnal; within 24 h all 30 immature spiders had constructed retreats and remained hidden during the light period, venturing out only during the dark period to forage/hunt. Pekár & Král (2001) recorded activity peaks for this species early in the morning from 0600–0900 h and in the evening from 1830–2200 h but did not monitor the nocturnal activity of this species. Couvreur (1990b) provides data indicating that this species is active at night. Entrance openings were visible on the retreats of some spiders while others plugged the entrance with rocks or soil particles. Of the 30 spiderlings, 16 were used for feeding experiments. Voucher specimens have been deposited in the arachnid collection at the Denver Museum of Nature & Science.

Three–four hours after the onset of the dark period the dishes were checked for spiders that had emerged from their retreats using a light with a red filter. In order to conduct feeding experiments, ants were gathered from another collecting site where *Z. rubidum* was also found off Easley Road on North Table Mesa in Golden, Colorado, Jefferson County

(39°46'31" N, 105°11'30" W, 1,762 m). These ants were identified as *Lasius niger* var. *americanus* (Emery 1893) (Formicinae) and *Myrmica* sp. (Myrmicinae). These ants are active both during the day and at night in the field (personal observation). We conducted 26 feeding trials among these 16 individuals. Although seven spiders were observed more than once, each of the 26 feeding trials was treated as an independent event since at least one week elapsed between trials.

For each trial, a single ant was placed into each of the dishes with an active spider and the behaviors of the spider and the ant were observed using a stopwatch to time events. These interactions were observed through an Olympus SZH stereo-microscope with a red acetate filter placed over the light source or over the Petri dish to minimize the influence the light may have had on the spiders' behavior.

The 16 spiderlings used in the feeding trials were divided into three arbitrary Size Classes: Size Class A included three juveniles 1.7–1.9 mm in length; Size Class B included nine spiderlings 2.0–2.2 mm in length; and Size Class C included four spiderlings 2.3–2.6 mm in length. In comparison, adult spiders ranged in size from 2.09–2.87 mm ($n = 8$; including four males and four females). We recorded the following data: 1) the time between the initial bite and reaction of the ant (immediate response, response 1–20 sec after bite, response 21–40 sec after bite); 2) the location of the initial bite (rear leg of ant, middle leg, front leg, antenna, abdomen, unknown); 3) the initial reaction of the ant to the bite; 4) subsequent reactions of the ant; 5) whether the spider bit more than once; and 6) the time from the initial bite to complete paralysis.

Prior to the encounters with the spiders, ants moved randomly around the Petri dish, antennating the substrate and sometimes picking up sand or other material with their mandibles. In 18/26 trials, the ant reacted immediately to the spider's bite, stopping its random movements and showing a distinct response; in 5/26 trials the ant reacted 1–20 sec after being bitten; in 3/26 trials initial reaction was 21–40 sec. In four of the trials, the attack by the spider was so rapid that it was not possible to determine with certainty where on the ant's body the initial bite was delivered. In the 22 attacks that could be scored, the ants were initially bitten more often on their rear legs (11/26 times) than on the middle legs (4/26 times), the front legs (5/26 times), the antennae (1/26 instances), or the abdomen (1/26 instances). Statistical analysis showed that the rear legs were bitten significantly more often than expected and the antennae were bitten significantly less often than expected by chance ($\chi^2 = 11.75$, d.f. = 4, $P < 0.02$). The most common initial response of the ant to the bite was to groom the affected appendage (18/26 trials). In 2/26 trials the initial

response was to autotomize or attempt to autotomize the bitten appendage; in 2/26 trials the initial response was body spasm; in 1/26 trials the ant shook the bitten leg; in 1/26 trials the initial response was rapid paralysis; and in 2/26 trials the initial response was not recorded (the time between bite and paralysis was too rapid).

Subsequent reactions to the bite included self-amputation, or autotomy, of the bitten limb, body spasms, abdominal contractions resulting in a twisting of the abdomen to the side, and, eventually, paralysis. In 4/26 trials, the ant autotomized the bitten limb between approximately 10 sec and 3.67 min from being bitten (mean \pm s.d.: 1.25 ± 1.63 min). In 12/26 of the trials, spiders bit the ants multiple times. In all but one trial, the attack by *Z. rubidum* resulted in complete paralysis of the ant. In that one trial, the ant autotomized the bitten leg within 15 sec of being bitten. After 17 min the ant was still active and apparently unaffected and the trial was ended.

The average time to complete paralysis was 7.85 min (s.d. = 4.72 min, $n = 25$). We decided to determine if the time to paralysis was influenced by the size of the spider as, presumably, larger spiders might deliver more venom. Therefore, we compared the mean time to paralysis for the three different Size Classes. The mean time to paralysis for Size Class A spiders was 8.35 ± 2.67 min ($n = 4$); the mean time to paralysis for Size Class B spiders was 6.77 ± 4.38 min ($n = 10$); and the mean time for Size Class C spiders was 8.67 ± 5.63 min ($n = 11$). We used the GT2 method for multiple comparisons of means for unequal sample sizes (Sokal & Rohlf 1981) and found no statistical difference in the time between initial bite and complete paralysis of the ant for the three Size Classes of spiders ($m_{.05[3,22]} = 2.584$, $P > 0.05$ for all pairwise comparisons).

Ants were bitten multiple times in all trials (4/4) with Size Class A spiders, in 2/9 trials with Size Class B spiders, and in 5/11 trials with Size Class C spiders. Ants autotomized the bitten appendage in two trials with Size Class B spiders and in one trial with a Size Class C spider (the fourth instance of autotomization resulted in no paralysis of the ant and was not included in the analysis). Since multiple bites and autotomization of the bitten limb may affect the time to paralysis, we eliminated these trials from the data set to determine if there was a difference in time to paralysis between the different spider Size Classes. In this comparison, the mean time to paralysis for Size Class B spiders was 5.33 ± 3.97 min ($n = 6$) and the mean time to paralysis for Size Class C spiders was 7.10 ± 7.60 min ($n = 5$) resulting in no significant difference in the time to paralysis ($m_{.05[1,9]} = 2.262$, $P > 0.05$). It is important to note that the size of the ants fed to the spiders was not measured. However, all ants

were 4 mm or less in length and, subjectively, appeared to be approximately similar in size.

From our observations of live *Z. rubidum*, it appears that spiders usually remained inside their retreats during the day, emerging to hunt ants at night. Upon encountering an ant, *Z. rubidum* typically bit a rear leg rather than a front appendage or the body of the ant. The ant usually reacted immediately to the bite by grooming the bitten appendage. In some instances, the ant autotomized the bitten appendage and, in one such instance, this autotomization of the leg apparently prevented the venom from paralyzing the ant. Often the spider re-approached the ant to deliver one or more additional bites. In all but the one instance mentioned above, the end result of these bites was complete paralysis of the ant.

Once the ant stopped moving, the spider approached and touched the ant with its first pair of legs. If the ant did not respond, the spider carried the ant to a secluded place (under a rock or near its retreat) using its fangs and palpal claws to carry the ant and began feeding on the ant. Couvreur (1990b) also reported the tendency of *Z. rubidum* to carry the ant to a secluded place for consumption. Couvreur (1990a) proposed that the spider used this paralyzed ant as a type of disguise and protection against attacks by other members of the ant colony when the spider foraged near the colony entrance.

Spiders of the family Zodariidae possess a series of one to 15 modified setae on the dorsolateral surface of the femora. These flattened setae have openings to secretory pores at the bases, and the hairs + pores are collectively referred to as the femoral organ (Jocqué 1988, 1991). Jocqué and Billen (1987) suggest that the femoral organ found on zodariids, particularly in the genus *Zodarion*, may be involved in prey capture. They suggest that the secretions produced by the femoral organ may act to subdue the ant. Santschi (1908) and Harkness (1976) indicate that an ant appeared to be subdued when a spider apparently touched the ant with the front legs and did not necessarily require a bite. However, our observations do not support the role of the femoral organ suggested by Jocqué and Billen (1987). In our experiments, paralysis of the ants ensued only after the spider bit one or more of the appendages (legs or antennae). Contact by the spider's front legs, as occurred on several instances when a spider first approached a passing ant, was not sufficient to subdue the ants. Jocqué (1988) and Couvreur (1990b) also indicate that a bite from the spider is necessary to subdue the ant. The attack by the spider, as pointed out by Harkness (1976), is often extremely rapid so that administration of a bite by the spider may not be clearly discernable unless the attack itself is observed with the aid of a microscope.

A variety of spiders engage in myrmecophagy. Ants are abundant in most terrestrial ecosystems

but, due to their defensive capabilities (Hölldobler & Wilson 1990), specialized capture techniques have evolved among many myrmecophages. Larger more robust myrmecophagic spiders, such as different species of jumping spiders (Salticidae), have been observed to position themselves facing their ant prey, attacking head-on (Edwards et al. 1975; Cutler 1980; Li et al. 1999). This frontal attack allows the spider to grasp the prey by the alitrunk making it difficult or impossible for the ant to defend itself. Spiders in the family Theridiidae rely on silk to capture ants, often building their webs in close proximity to ant nests (Hölldobler 1970, Porter & Eastmond 1981; MacKay 1982; Clark 1996). *Euryopsis coki* Levi 1954 was observed securing a worker of *Pogonomyrmex* with a strand of silk then biting it on the leg while the ant was tethered to the ground (Porter & Eastmond 1981). In contrast, the small size of *Zodarion* spiders makes frontal attacks impractical and risky and silk is not used by these spiders to immobilize the prey. Spiders of the genus *Zodarion* (Zodariidae) have, instead, adopted a hit and run approach to hunting ants, composed of an attack to the rear appendages and a short withdrawal until the ant becomes paralyzed (Schneider 1971; Harkness 1976, 1977; Couvreur 1990b; present study).

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